

Review of *Copadichromis* (Teleostei: Cichlidae) with the description of a new genus and six new species

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The status of the genus *Copadichromis* is discussed. *Copadichromis prostoma* and *C. boadzulu* are placed in *Nyasachromis*. *Copadichromis cyclicos*, *C. thinos*, *C. conophoros*, *C. flavimanus*, *C. inornatus*, and *C. eucinostomus* are placed in *Mchenga*, new genus, diagnosed principally on morphology, bower construction, and habitat preference. In the remaining *Copadichromis*, three species groups are identified, the *C. quadrimaculatus* group, the *C. mbenjii* group, and the *C. virginalis* group. Six new species are described in the *C. mbenjii* group: *C. melas*, *C. chizumuluensis*, *C. diplostigma*, *C. insularis*, *C. cyanocephalus*, and *C. parvus*.

Introduction

Eccles & Trewavas (1989) diagnosed the haplochromine genus *Copadichromis* (type species *Haplochromis quadrimaculatus*) from Lake Malaŵi by a small mouth, weak jaws, small recurved simple or bicuspid teeth, and elongated premaxillary pedicels that can be extended forward forming a protrusible mouth. All members of *Copadichromis* are plankton feeders. The genus initially contained 17 species, including seven species originally described by Trewavas (1935) of which six (*Haplochromis eucinostomus*, *H. inornatus*, *H. cyaneus*, *H. prostoma*, *H. chrysonotus*, *H. quadrimaculatus*) were described as sharing a protractile mouth and *H. pleurostigma*, and 10 species (*H. flavimanus*, *H. mloto*, *H. virginalis*, *H. boadzulu*, *H. trimaculatus*, *H. nkatae*, *H. jacksoni*, *H. borleyi*, *H. pleurostigmoides*,

H. likomae) described by Iles (1960). Subsequently, Konings (1990, 1999) described *C. azureus*, *C. mbenjii*, *C. verduyni*, *C. trewavasae*, *C. ilesi*, and *C. geertsi*. *Copadichromis conophoros*, *C. cyclicos*, *C. thinos*, and *C. atripinnis* were described by Stauffer et al. (1993) and Stauffer & Sato (2002).

Stauffer et al. (2002) argued that behavioral traits are important diagnostic tools for determining phylogenetic relationships among Lake Malaŵi cichlids. Important behavioral traits among the plankton-feeding cichlids are the structural characteristics and the position in habitat of the spawning and display sites. The purpose of this paper is to reexamine the genus *Copadichromis*, to describe a new genus with some of its diagnostic characters based on behavioral traits, and to describe six new species.

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Methods

Fishes were collected by the authors in Lake Malaŵi (Fig. 1) by chasing them into a monofilament net while SCUBA diving. Fishes were anesthetized with clove oil, preserved in 10 % formalin, and placed in 70 % ethanol for permanent storage. All counts and measurements were made on the left side of the fish, with the exception of gill-raker counts. Counts and measurement follow Barel et al. (1977) and Stauffer (1991, 1994) with the following exceptions. Head depth was measured from the hyoid symphysis to the top of the (non-expanded) head at a 90° angle to the horizontal body axis (horizontal line drawn through the lower part of lateral line). Body depth was measured from the dorsal-fin origin to the ventral outline of the fish at a 90° angle to the horizontal body axis. The pre-orbital depth was measured as the length of the intersection of the lachrymal bone with a line continuing the radius of the orbit and parallel to the snout profile, dissecting the lachrymal bone (Eccles & Trewavas, 1989). Caudal base is defined as the area between the caudal fin and the caudal peduncle. Institutional abbreviations follow Leviton et al. (1985), except UMBC, University of Malaŵi, Bunda College.

Pigmentation pattern was recorded in the field, in territorial and non-territorial males, females, and juveniles. The conspicuous spots on the body homologous to those exhibited by females and immatures (in those species that have spots) are often overlain by the breeding coloration of territorial males. The position of the spots on the flank is similar in most *Copadichromis* examined. A supra-pectoral spot is normally located below the 9-12th scale from the head, above the horizontal body axis and below, but sometimes in contact with, the upper lateral line. A supra-anal spot is normally located between the upper and lower lateral line above the anal fin and a caudal spot is normally found on the base of the caudal, but sometimes extending onto the caudal peduncle. The color pattern of the anal fin in breeding males differs among the various species and we make a distinction in the width of the distal marginal band. The color of the marginal band varies somewhat between males of the same population but in the diagnosis we refer to them as a yellow margin even though the color ranges, among all examined species, between whitish-yellow and orange. We distinguish

three classes in the width of such a marginal band: wide, narrow, and no marginal band. A wide band covers 20-50 % of the depth of the anal fin; a narrow band covers between 1-10 % of the fin. The different pigmentation patterns are variable in almost all species examined and in the descriptions such variation is recorded by placing a slash between the two colors between which the specific pattern varies, i.e. blue/white is used to designate that the color ranges from blue to white and includes intermediate shades in certain individuals.

Morphometric data were analyzed using sheared principal component analysis (SPCA), with the covariance matrix factored (Humphries et al., 1981; Bookstein et al., 1985). Meristic data were analyzed with principal component analysis (PCA), with the correlation matrix factored. Differences among species were illustrated by plotting the sheared second principal components of the morphometric data against the first principal components of the meristic data (Stauffer & Hert, 1992). If the minimum polygon clusters resulting from such plots overlapped, we first determined if the clusters were significantly different along one axis, independent of the other. In such cases, a Duncan's multiple range test ($p < 0.05$) was used to determine which clusters differed from each other. If the clusters were not significantly different along one axis independent of the other, then a MANOVA, in conjunction with a Hotelling-Lawley trace, was used to determine whether the mean multivariate scores of clusters formed by the minimum polygons of the PCA scores were significantly different ($p < 0.05$) (Stauffer et al., 1997).

Theoretically, we believe that the evolutionary species concept is the only species concept that provides us with a basis to circumscribe species (Stauffer & McKaye, 2001). Because the evolutionary species concept is non-operational, we must use one of the many other species concepts (see Mayden 1997) as a surrogate (i.e., we use the biological species concept as a surrogate if sympatric forms mate assortatively, in which case we regard them as distinct species). We rely heavily on morphological differences in assessing specific status of these forms. In cases where we could not find definitive non-overlapping morphological characters to delimit species, we relied on multivariate analyses to aid us in distinguishing species. Realizing that morphometric differences normally exist between allopatric populations,

we further based our distinction between species on male breeding coloration, behavioral traits, and presence of distributional intermediate forms.

Taxonomic analysis

Copadichromis Eccles & Trewavas

Type species. *Haplochromis quadrimaculatus* Regan, 1922.

Diagnosis. *Copadichromis* is comprised of small to medium-sized plankton-feeding cichlids endemic to Lake Malaŵi, frequenting open water and rocky habitats. A small mouth, weak jaws, small recurved simple or bicuspid teeth in juveniles and females, elongated premaxillary pedicels that can be extended forward forming a protrusible mouth, small, compressed teeth on the lower pharyngeal bone, and an elevated number (12-28) of rakers on the first ceratobranchial separate *Copadichromis* from all other described Lake Malaŵi genera. Species of *Copadichromis* breed in association with rocks. Territorial males either defend rocky spawning sites or construct bowers at the sand/rock interface of which rocks or a single stone form an integral part.

When Eccles & Trewavas (1989: 295) described *Copadichromis* they already suggested that this genus is possibly not monophyletic and "that its specialisations are the result of convergence in two or more lineages." Konings (1990) suggested moving some of the species to *Nyassachromis*, on the basis of differences in the basic melanin pattern. These patterns play a major role in distinguishing the various genera of Malaŵi cichlids. Stauffer et al. (1993) rejected this proposal on the basis of incompatibility with the intestinal morphology of some members of latter genus, but suggested the creation of a *C. eucinostomus* group within *Copadichromis*. A phylogeny based on mitochondrial DNA (Moran et al., 1994; Turner et al., 2004) was found consistent with the general consensus that *Copadichromis* is polyphyletic.

Based on morphological and behavioral differences, we propose that *Copadichromis*, as it is currently conceived, is comprised of at least five discernable groups of plankton-feeding cichlids. Two characters, a mid-lateral band and a narrow caudal peduncle, align two species (*C. prostoma*,

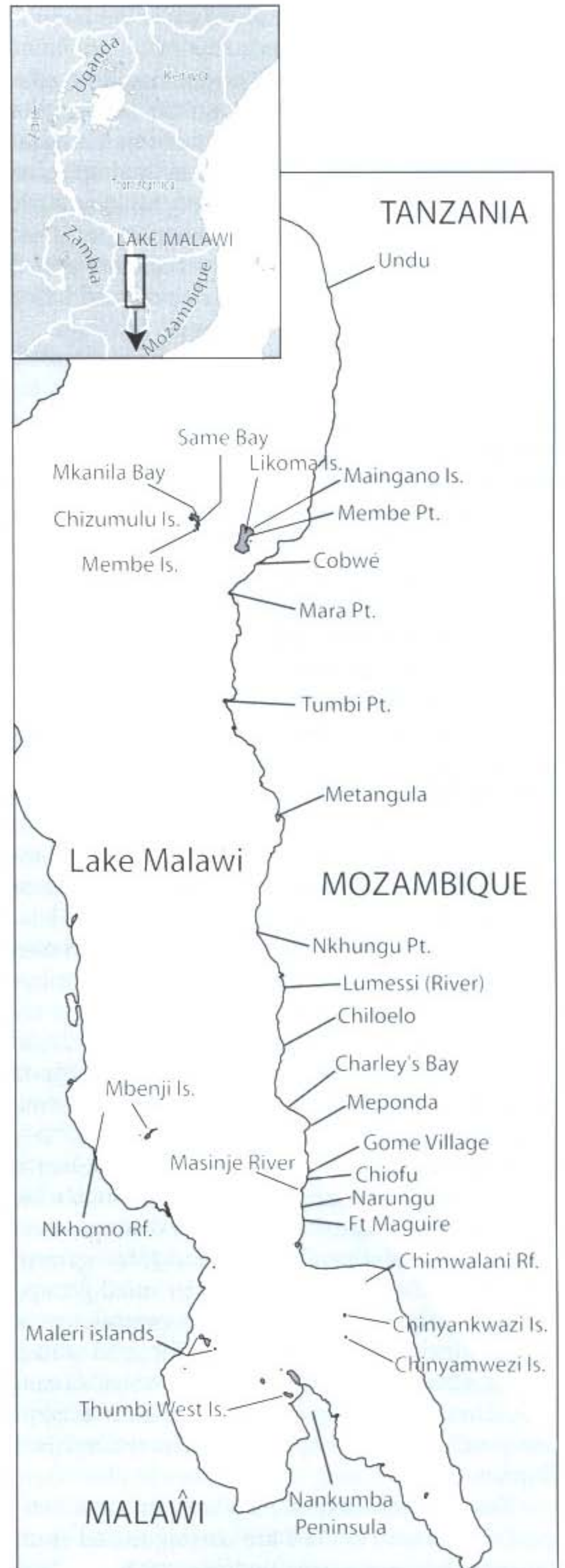


Fig. 1. Southern Lake Malaŵi showing collection sites.

C. boadzulu) with *Nyassachromis* and we include them in that genus.

A group of species is distinguished by a relatively low number of rakers on the first ceratobranchial (10-18), by bicuspid teeth in the outer row of the oral jaws, and by a lack of spots or stripes on the body. Members of this group are further distinguished by the construction of the bower which does not include a rock and which is normally constructed on the open sand. This group is described as a new genus, *Mchenga*.

A group in *Copadichromis* is distinguished by a relatively high number of gill rakers (19-28), by unicuspid teeth in the outer row of the oral jaws of males, and by spots (supra-pectoral, supra-anal, and/or caudal) on the flanks of juveniles. In some populations of *C. quadrimaculatus* and *C. borleyi* some or all of such spots are lost in adult individuals. Members of this group, designated as the *C. quadrimaculatus* group, are further distinguished by their breeding territories in pure rocky habitats, either in caves (*C. nkatae*), on large boulders (*C. quadrimaculatus*, *C. cyaneus*, *C. trimaculatus*, *C. jacksoni*, *C. borleyi*; Fig. 2a), in the water column above rocks (*C. chrysonotus*), or in deep rocky habitats (deeper than 25m) where the sandy bottom constitutes less than 10 % of the exposed substratum (*C. pleurostigmoides*, *C. geertsi*). Mouthbrooding females usually school in mid-water or find shelter in groups alongside large boulders, but are rarely found gathering near the bottom as is the case with species of the following group.

The *C. mbenjii* group possesses a relatively low number of ceratobranchial rakers (12-20), unicuspid teeth in the outer row of the oral jaws of males, and spots on the flank (supra-pectoral, supra-anal, and/or caudal). Members of this group build sand bowers of which a rock or a stone forms an integral part (Figs. 3b, 5b, 6b, 8b, 9b, and 11b) and can thus further be distinguished from those of the *C. quadrimaculatus* group. Mouthbrooding females gather in small groups and normally remain within a few centimeters of the bottom; they are rarely found in mid-water. The *C. mbenjii* group includes: *C. mbenjii*, *C. azureus*, *C. verduyni*, *C. trewavasae*, *C. atripinnis*, *C. pleurostigma*, and six new species which are described herein.

The members of the *C. virginalis* group (*C. virginalis*, *C. mloto*, *C. ilesi*) are distinguished from the other two groups in *Copadichromis* by the lack of conspicuous markings on the body (also in juveniles), and from *Mchenga* by a relatively high

number of ceratobranchial rakers (21-25 vs. 10-18) and unicuspid teeth in the outer row of the premaxilla. Some members of this group construct bowers against a rock (*C. ilesi*, *C. mloto*, and a number of undescribed forms) while *C. virginalis* (or a form belonging to this group that closely resembles it; observation at Higga Reef, Tanzania; 11°18.380'S 34°44.791'E; February 2005) breeds in the rocky habitat on large boulders. Mouthbrooding females usually school in mid-water or find shelter in shoals alongside large boulders, but are rarely found gathering near the bottom.

The members of the *C. quadrimaculatus* and the *C. mbenjii* groups can be distinguished from the plankton-feeding *Ctenopharynx*, possibly a closely related genus, by the shape and position of the supra-pectoral spot. In *Ctenopharynx*, the supra-pectoral spot has a squarish shape, is situated on the upper lateral line, and exhibits an elongate extension. In *Copadichromis*, the supra-pectoral spot is round or elliptic, situated below the upper lateral line, and shows no irregular extensions.

The generic placement of *C. likomae* is problematic. It resembles the members of the *C. quadrimaculatus* group and the *C. mbenjii* group because it has a distinct supra-pectoral and caudal spot, but it differs from them by the structure of its bower which is built on sandy bottoms and does not integrate a rock. We will retain it in this genus until the interrelationships within *Copadichromis* are elucidated.

Copadichromis mbenjii group

The *C. mbenjii* group is comprised of a series of small cichlid fishes that all have a supra-pectoral and a caudal spot, and all but *C. diplostigma* and most *C. pleurostigma*, a supra-anal spot. In breeding males, such spots are usually overlain by the intense breeding coloration. The members of this group frequent habitats characterized by sandy bottoms with scattered rocks and stones. The sandy bottoms in such habitats comprise 50-90 % of the exposed substratum. Members of this group build sand bowers of which a rock or a stone forms an integral part (Figs. 3b, 5b, 6b, 8b, 9b, and 11b). Species of the *C. mbenjii* group have 12-20 gill rakers on the first ceratobranchial, a slender lower pharyngeal jaw with many small bicuspid teeth, a more elongate body, and a shorter premaxillary pedicel than those of the *C. quadri-*

maculatus group, but all three characters show overlap. In general, species of the *C. mbenjii* group forage close to the bottom and include benthic invertebrates in their diets, while species of the *C. quadrimaculatus* group forage in the water column and feed almost exclusively on zooplankton. The breeding behavior of *C. pleurostigma* is unknown but on the basis of its melanin pattern, a large supra-pectoral spot and a small, usually barely visible, supra-anal, and caudal spot, and relatively small number of gill-rakers (17-18), we include it in this group. The supra-pectoral spot in *C. pleurostigma* is usually more than 5-10 times the diameter of the supra-anal or caudal spot, when latter spots are present.

***Copadichromis mbenjii* Konings**
(Fig. 2b)

Copadichromis mbenjii Konings, 1990: 116 (Malawi: Mbenji Island).

Material examined. PSU 3641, 19, UMBC 5, 1, 72.6-104.4 mm SL; Malawi: Lake Malawi: Mbenji Island, 13° 26.379'S 34° 29.546'E; J. R. Stauffer & A. F. Konings, 28 Feb 2002.

Diagnosis. *Copadichromis mbenjii* is distinguished from other members of the *C. mbenjii* group by the possession of three lateral spots on the body (vs. two in *C. diplostigma* and one in *C. pleurostigma*) and a supra-pectoral spot that is 2-2.5 times the diameter of the supra-anal spot (vs. 1-1.5 times in all other members of this group except *C. diplostigma*, which lacks a supra-anal spot, and *C. chizumuluensis*). It is distinguished from *C. chizumuluensis* by 12-15 gill rakers (vs. 17-19) on the first ceratobranchial. Breeding males are distinguished from those of most other species in the *C. mbenjii* group by a yellow breast (vs. blue in *C. azureus*, *C. atripinnis*, *C. chizumuluensis*, *C. insularis*, *C. cyanocephalus*, *C. parvus*, and *C. pleurostigma* or black in *C. trewavasae* and *C. melas*) and from those of *C. diplostigma* by a wide yellow marginal band in the anal fin (vs. a narrow band in *C. diplostigma*) and those from *C. verduyni* by a distinct yellow margin of the dorsal fin (vs. white in *C. verduyni*).

Description. Morphometric and meristic data in Table 1. Dorsal head profile convex, with a slight concavity between eye and snout tip in large

males, convex in females and immatures. Gape inclination of mouth about 40° to horizontal; jaws isognathous. Teeth in three rows on dentary and premaxilla; outer row teeth bicuspid in females and immatures, unequally bicuspid tending to unicuspid in mature males; inner rows unicuspid. Lower pharyngeal jaw small, all teeth bicuspid; posterior two central teeth sometimes slightly enlarged. Gill-rakers on ceratobranchial short and broad-based.

Coloration. Breeding males: head blue; throat white with gray patches. Lateral portion of body light-blue suffused with orange, anterior portion of scales orange/brown and posterior edge of scales light-blue. Nape orange/brown. Breast yellow with blue/gray spots; belly gray with blue/white highlights. Dorsal membranes blue with orange/brown markings; membranes between rays with orange/brown spots and streaks; spines and rays blue proximally and gray/blue distally; narrow black submarginal band with white lappets and yellow tips. Caudal fin with blue rays and yellow/orange membranes. Proximal half of anal fin blue/black; distal half yellow; posterior half of anal fin with white ocelli. Pectoral fin clear. Pelvic fins yellow/brown with white leading edge and dark band between first and second ray.

Females: head gray/purple; cheeks silvery with purple highlights; opercle silver with brown and purple highlights and black opercular spot. Throat white. Lateral portion of body with three black spots: supra-pectoral spot below 9-10th scale in contact with upper lateral line and about two times size of supra-anal spot; supra-anal spot at 21-23rd scale above and in contact with lower lateral line and covering 2-3 scales; caudal spot same diameter as supra-anal spot on caudal base; above upper lateral line bronze ground color with purple highlights; below upper lateral line silver ground color with center of each scale yellow/brown. Four vertical bars between supra-pectoral spot and dorsal-fin origin. Breast and belly white. Dorsal fin clear with orange/brown spots, white lappets, and orange/brown tips. Caudal fin gray/yellow with orange/brown spots. Proximal two-thirds of anal fin light gray, distal one-third clear with orange/brown ocelli and narrow orange/brown edge. Pectoral fin clear. Pelvic fin clear with gray membrane between first two rays.

Distribution and field observations. *Copadichromis mbenjii* is endemic to Mbenji Island in the southern portion of Lake Malawi (Fig. 1).

It occurs in the sand/rock interface at depths of 7-19 m. Territorial males build a bowl-shaped

bower beneath and/or adjacent to a rock, with a diameter of 18-42 cm and a rim that is 4-7 cm high. The rock used for the bower has a size that varies between one-fifth of the bowl's diameter to a size slightly larger than the bowl. The rim

Table 1. Morphometric and meristic values of *Copadichromis mbenjii* from Mbenji Island, *C. azureus* from Mbenji Island, *C. verduyni* from Chiofu, and *C. trewavasae* from Likoma Island (paratypes) and Chizumulu Island.

	<i>C. mbenjii</i>	<i>C. azureus</i>	<i>C. verduyni</i>	<i>C. trewavasae</i>	
	(n=20)	(n=20)	(n=20)	paratypes (n=6)	Chizumulu Island (n=18)
Standard length, mm	72.6-104.4	69.9-117.1	67.8-88.5	56.6-103.5	76.7-104.5
Head length, mm	21.7-30.8	22.1-36.0	22.2-29.1	17.8-31.7	24.7-35.0
Percent standard length					
Head length	27.8-33.3	29.9-32.9	31.5-35.3	29.8-32.8	31.9-33.6
Body depth	34.0-37.9	33.0-38.7	34.4-38.4	31.4-38.8	33.5-38.3
Snout to dorsal-fin	32.5-57.5	32.4-36.4	35.8-39.3	33.4-38.1	32.4-36.0
Snout to pelvic-fin	36.1-50.4	34.8-41.1	38.4-43.1	35.4-40.0	37.9-43.6
Dorsal-fin base length	55.9-61.3	55.7-60.1	55.9-59.0	54.6-59.0	54.5-57.4
Anterior dorsal to anterior anal	50.3-55.3	49.9-55.4	50.2-54.6	48.1-54.2	48.6-54.9
Anterior dorsal to posterior anal	60.2-65.5	60.2-63.7	58.7-63.8	59.1-63.1	58.4-64.4
Posterior dorsal to anterior anal	29.4-34.2	30.2-33.8	29.4-34.6	28.2-32.9	30.3-33.1
Posterior dorsal to posterior anal	15.6-17.1	14.8-17.6	15.1-18.5	14.8-17.0	15.8-17.6
Posterior dorsal to ventral caudal	17.9-20.6	17.5-20.8	17.6-21.0	17.4-20.4	17.6-20.4
Posterior anal to dorsal caudal	19.5-22.5	20.6-24.9	19.3-23.6	20.2-23.4	20.3-22.9
Anterior dorsal to pelvic-fin origin	36.0-39.6	35.2-40.4	36.6-42.4	32.0-40.7	32.3-39.3
Posterior dorsal to pelvic-fin origin	55.4-61.1	35.9-60.4	52.7-58.4	53.7-63.4	54.9-59.2
Caudal peduncle length	14.8-17.8	14.3-19.8	14.8-17.5	14.2-18.3	15.3-18.9
Least caudal peduncle depth	11.1-13.4	11.5-13.2	11.3-13.6	10.6-12.4	11.5-12.5
Percent head length					
Snout length	26.6-31.8	26.3-32.9	27.4-34.6	25.9-33.5	25.6-34.3
Postorbital head length	33.3-36.9	35.5-38.8	34.5-49.8	32.7-40.4	32.8-35.5
Horizontal eye diameter	36.0-42.3	31.6-39.8	33.3-39.7	29.5-40.5	30.7-36.4
Vertical eye diameter	35.1-42.8	31.1-39.0	32.9-39.7	29.1-40.3	29.3-36.2
Head depth	92.0-107.9	88.7-111.1	86.0-103.3	82.7-106.5	88.1-102.3
Preorbital depth	13.7-18.1	12.4-19.6	15.1-20.5	11.7-20.1	14.9-18.6
Cheek depth	15.2-25.7	14.4-26.3	14.8-23.9	11.3-24.1	17.7-26.5
Lower jaw length	35.2-42.1	31.9-41.1	36.0-42.0	32.9-42.4	32.6-39.8
Counts					
Dorsal-fin spines	16-18	15-18	16-17	15-17	16-17
Dorsal-fin rays	10-11	10-12	9-11	9-11	10-11
Anal-fin spines	3	3	3	3	3
Anal-fin rays	8-9	8-9	7-9	8-9	8-9
Pelvic-fin rays	5	5	5	5	5
Pectoral-fin rays	13-14	12-14	13-14	13-14	13
Lateral line scales	33-34	32-35	31-34	31-34	32-34
Pored scales posterior to lateral line	1-3	1-2	1-2	1-3	2
Scale rows on cheek	2-3	2-3	2	2-3	2
Gill rakers 1 st ceratobranchial	12-15	14-19	12-15	15-17	14-17
Gill rakers 1 st epibranchial	3-5	5-6	3-5	4-6	5-7
Teeth outer left lower jaw	10-15	10-17	10-13	10-14	11-12
Teeth rows upper jaw	3	3-4	3	3	3
Teeth rows lower jaw	3	3-4	3	3	3

normally encompasses more than half a circle and the center of the bowl is located beneath the rock. The small cave created under the rock is used as the spawning site. Females occur in schools numbering up to 50 individuals and remain within 2 m above the bottom. Males and females feed on plankton in the water column and on benthic invertebrates.

Copadichromis azureus Konings

(Fig. 2c)

Copadichromis azureus Konings, 1990: 112 (Malawi: Mbenji Island).

Material examined. PSU 3642, 20, 69.9-117.1 mm SL; Malawi: Lake Malawi: Mbenji Island, 13°26.379'S 34°29.546'E; J. R. Stauffer & A. F. Konings, 28 Feb 2002.

Diagnosis. *Copadichromis azureus* is distinguished from other members of the *C. mbenjii* group by the possession of three lateral spots on the body (vs. two in *C. diplostigma* and one in *C. pleurostigma*), a supra-pectoral spot that is about 1.5 times the supra-anal spot (vs. 2-2.5 times in *C. mbenjii* and *C. chizumuluensis* and about the same size as the supra-anal spot in *C. melas*, *C. cyanocephalus*, and *C. parvus*), a supra-pectoral spot that is separate from the upper lateral line (vs. in contact with the upper lateral line in *C. verduyni* and *C. insularis*), a supra-anal spot which is smaller than two scales (vs. three scales or more in *C. verduyni*, *C. trewavasae*, and *C. atripinnis*). Male *C. azureus* in breeding coloration are distinguished from those of other species in the *C. mbenjii* group by a blue breast (vs. yellow in *C. mbenjii*, *C. diplostigma*, and *C. verduyni* or black in *C. trewavasae* and *C. melas*) and by a narrow yellow marginal band in the anal fin (vs. a wide marginal band in *C. atripinnis*, *C. cyanocephalus*, *C. pleurostigma*, and *C. insularis*; vs all black anal without colored margin in *C. melas* and *C. parvus*). Males are distinguished from those of *C. chizumuluensis* by the lack of any spots or streaks in the anal fin.

Description. Morphometric and meristic data in Table 1. Dorsal snout profile straight; gape inclination of mouth about 40° to horizontal; jaws isognathous. Teeth on dentary and premaxilla in 3-4 rows; outer row teeth unicuspid and somewhat enlarged in mature males (> 80 mm SL), and bicuspid in females and immature males. Lower

pharyngeal jaw small, dentigerous area notched posteriorly, with bicuspid teeth, all small or with few median teeth slightly enlarged. Gill-rakers on ceratobranchial short and slender.

Coloration. Breeding males: head blue with green highlights; interorbital blue with light-blue highlights; blue opercle; throat gray with blue highlights. Lateral portion of body dark blue ground color dorsally, fading to blue/gray ventrally; eight dark gray bars. Breast and belly greenish blue with dark-gray markings. Dorsal fin dark blue with green and light-blue highlights; white marginal band with yellow/white lappets. Caudal fin with blue rays and blue/green membranes; distal one fourth dark gray. Anal fin blue to green/blue with very narrow marginal orange/yellow band. Pectoral fin with gray rays and clear membranes. Pelvic fin with blue/green rays and blue/gray membranes.

Females: head gray dorsally, fading to white ventrally; blue and silver highlights on cheek; throat white. Lateral portion of body gray/blue ground color with anterior portion of scale outlined in orange/yellow. Three distinct black spots on lateral portion of body: supra-pectoral spot below 10-12th scale not in contact with upper lateral line and about 1.5 times size of supra-anal spot; supra-anal spot at 23-25th scale above and in contact with lower lateral line and covering less than two scales; caudal spot same diameter as supra-anal spot on caudal base; eight gray bars and white belly with gray highlights. Three vertical bars between supra-pectoral spot and dorsal-fin origin. Dorsal fin clear with pale orange/gray vermiculations in rayed portion; orange lappets. Caudal fin with clear rays and orange/gray membranes. Anal fin clear with scattered micro-melanophores; 6-8 pale orange ocelli and orange lappets between rays. Pectoral fin clear. Pelvic fin clear with light-gray membrane between first and second ray.

Distribution and field observations. *Copadichromis azureus* inhabits the sand/rock interface around Mbenji Island and at Nkhomo Reef (Fig. 1; 13°19.517'S 34°21.419'E).

Most territorial males defend their bowers at a depth of 19-25 m. The bowl in front of the spawning cave spans about half a circle or less and is comprised of the sand that was excavated underneath the rock. Males never have been observed carrying sand from the surroundings

to enhance the bower, a behavioral trait that is commonly observed in the sympatric *C. mbenjii*. The entrance to the spawning cave has a height of 3.5–6.5 cm and the bower has a diameter of 19–33 cm. Individual bowers are 3–10 m apart. Females gather in small groups or are solitary, and feed from the plankton and benthic invertebrates near the bottom.

Copadichromis verduyni Konings
(Fig. 2d)

Copadichromis verduyni Konings, 1990: 118 (Malawi: Fort Maguire).

Material examined. PSU 3643, 20, 67.8–88.5 mm SL; Malawi: Lake Malawi, Chiofu Bay, 13°31.714'S 34°51.864'E; J. R. Stauffer & A. F. Konings, 11 Feb 2002.

Diagnosis. *Copadichromis verduyni* is distinguished from other members of the *C. mbenjii* group by the possession of three lateral spots on the body (vs. two in *C. diplostigma* and one in *C. pleurostigma*), a supra-pectoral spot that is about 1.5 times the supra-anal spot (vs. 2–2.5 times in *C. mbenjii* and *C. chizumuluensis* and about the same size as the supra-anal spot in *C. melas*, *C. cyanocephalus*, and *C. parvus*), and a supra-pectoral spot that is in contact with the upper lateral line (vs. separate from the upper lateral line in *C. azureus*, *C. cyanocephalus*, *C. parvus*, and *C. melas*). It is distinguished from *C. insularis* by a supra-anal spot that is separate from the upper lateral line (vs. in contact with it in *C. insularis*). It is distinguished from *C. atripinnis* by the lack of a narrow black submarginal band in the dorsal fin. Female *C. verduyni* cannot reliably be distinguished from those of *C. trewavasae*. Breeding males are distinguished from those of most other species in the *C. mbenjii* group by a yellow breast (vs. blue in *C. azureus*, *C. atripinnis*, *C. chizumuluensis*, *C. insularis*, *C. cyanocephalus*, *C. parvus*, and *C. pleurostigma* or black in *C. trewavasae* and *C. melas*) and from those of *C. diplostigma* by a wide yellow marginal band of the anal fin (vs. a narrow band in *C. diplostigma*) and from those of *C. mbenjii* by a white margin of the dorsal fin (vs. yellow in *C. mbenjii*).

Description. Morphometric and meristic data in Table 1. Dorsal snout profile straight to slightly convex in smaller individuals; gape inclination of mouth about 30° to horizontal; jaws isogna-

thous. Teeth on dentary and premaxilla in three rows; outer row teeth bicuspid in females and immatures, unequally bicuspid tending to unicuspid in mature males; inner rows teeth bicuspid in females and immature males, and unicuspid in mature males. Lower pharyngeal jaw small, dentigerous area notched posteriorly, with bicuspid teeth, all small, except posterior row slightly enlarged with few enlarged central teeth. Gill-rakers on ceratobranchial short and broad.

Coloration. Breeding males: head dark blue with light-blue highlights; interorbital blue with green patches; upper and lower jaws green; throat blue/green. Lateral portion of body blue dorsally fading to green/orange ventrally; anterior portion of scales orange; breast dark yellow; belly off white with orange and green highlights. Dorsal fin blue with white marginal band. Caudal fin with blue rays with micro-melanophores and orange membranes. Anal fin with orange marginal band, membranes between spines blue. Pectoral fin clear. Pelvic fin black with white leading edge.

Females: head gray dorsally, fading to white ventrally; white throat. Lateral portion of body gray ground color dorsally fading to white ventrally with gold spot on anterior portion of each scale; supra-pectoral spot below 11–12th scale in contact with upper lateral line and about 1.5 times size of supra-anal spot; supra-anal spot at 22–23rd scale between upper and lower lateral line and covering 2–3 scales; caudal spot same diameter as supra-anal spot on caudal base extending onto peduncle; 2–3 vertical bars between supra-pectoral spot and dorsal-fin origin. Dorsal fin clear with brown/orange vermiculations. Caudal fin clear with orange/brown spots. Anal fin clear with some black pigment in rays. Pectoral fin clear. Pelvic fin clear with micro-melanophores.

Distribution and field observations. *Copadichromis verduyni* occurs along the eastern shores of Lake Malawi between Chimwalani Reef (Eccles Reef; 13°46.272'S 34°57.695'E) and Gome Village (Fig. 1; 13°30.535'S 34°52.007'E).

Among congeners, most territorial male *C. verduyni* defend the least-visible spawning sites. Sometimes the spawning caves have a rocky bottom and lack a sand-bowl entrance entirely. In many cases, however, small amounts of sand are moved to form a bower from the bottom of the little caves in which spawning takes place. In the

northern part of its distribution, it shares the sand/rock interface with *C. atripinnis*, but the latter is almost always found at deeper levels than *C. verduyni* and in more open habitat. Most male *C. verduyni* defend spawning sites at depths of 9-15 m. Females and non-territorial males feed from the plankton in the water column 1-3 m off the bottom and on benthic invertebrates.

Copadichromis trewavasae Konings

(Fig. 2e)

Copadichromis trewavasae Konings, 1999: 64 (Malawi: Likoma Island: Membe Point).

Material examined. MRAC 99097-P-2-3, 6 paratypes, 56.6-103.5 mm SL; Malawi: Lake Malawi: Likoma Island, Membe Point; Konings, 1 May 1989. – PSU 3634, 18, 76.7-104.5 mm SL; Malawi: Lake Malawi: Chizumulu Island: Membe Island, 12°02.947'S 34°36.930'E; J. R. Stauffer & A. F. Konings, 20 Feb 2002.

Diagnosis. *Copadichromis trewavasae* is distinguished from other members of the *C. mbenjii* group by the possession of three lateral spots on the body (vs. two in *C. diplostigma* and one in *C. pleurostigma*), a supra-pectoral spot that is about 1.5 times the supra-anal spot (vs. 2-2.5 times in *C. mbenjii* and *C. chizumuluensis* and about the same size as the supra-anal spot in *C. melas*, *C. cyanocephalus*, and *C. parvus*), a supra-pectoral spot that is in contact with the upper lateral line (vs. separate from the upper lateral line in *C. azureus*, *C. cyanocephalus*, *C. parvus*, and *C. melas*), and a supra-anal spot that is separate from the upper lateral line (vs. in contact in *C. insularis*). It is distinguished from *C. atripinnis* by the lack of narrow black submarginal band in the dorsal fin. Female *C. trewavasae* cannot be reliably distinguished from those of *C. verduyni*. Male *C. trewavasae* in breeding coloration are distinguished from those of the other members of the *C. mbenjii* group by a black ventral body and a blue to white blaze on the dorsum above the lateral line until the posterior end of the dorsal fin and continuing onto the upper margin of the caudal fin. The only other species in this group with a similar coloration is *C. parvus* in which a much smaller white-blue blaze does not extend beyond the dorsal fin.

Description. Morphometric and meristic data in Table 1. Dorsal snout profile straight; gape incli-

nation of mouth about 35° to horizontal; jaws isognathous. Teeth on dentary and premaxilla in 2-4 rows; outer tooth row containing unequally bicuspid teeth, inner rows unicuspid or unequally tricuspid in females and immature males; outer row teeth with large unicuspid teeth in mature males. Lower pharyngeal jaw small, dentigerous area notched posteriorly, with small bicuspid teeth. Gill-rakers on ceratobranchial short and broad.

Coloration. Breeding males: head black and blue/white interorbital blaze extending posteriorly to caudal fin. Lateral portion of body, dark blue/black ground color with light blue and gray highlights; breast and belly black; blue/white blaze on dorsum above lateral line until posterior end of dorsal fin. Proximal two-thirds of spinous dorsal fin blue/black with light blue highlights; distal one-third white. Proximal three-fourths of anterior three membranes of rayed portion of dorsal fin blue/black; distal one-quarter white; posterior membranes blue/black with orange tips. Proximal three-fourths of caudal fin black; distal one-fourth dark gray. Anal fin black with white/orange tips. Pelvic fin black with blue leading edge. Pectoral fin with black rays and clear membranes.

Females: head gray; silver cheeks and opercles with dark blue opercular spot and white throat. Lateral portion of body with three black spots: supra-pectoral spot below 9-11th scale not in contact with upper lateral line and about 1.5 times size of supra-anal spot; supra-anal spot at 23-25th scale above and in contact with lower lateral line and covering 2-3 scales; caudal spot same diameter as supra-anal spot on caudal base and onto peduncle. Three vertical bars between supra-pectoral spot and dorsal-fin origin. Above upper lateral line gray; below upper lateral line silver with posterior margins of scales blue. Belly and breast white. Spinous portion of dorsal fin gray with white lappets and orange tips. Rayed membranes gray with orange/brown spots. Caudal fin gray; anal fin hyaline with gray bar located approximately two-thirds of distal portion. Pelvic fin hyaline with first ray and membrane gray. Pectoral fin clear.

Distribution and field observations. *Copadichromis trewavasae* occurs along the rocky shores of Likoma and Chizumulu islands (Fig. 1). Several populations of a species that resembles *C. trewa-*

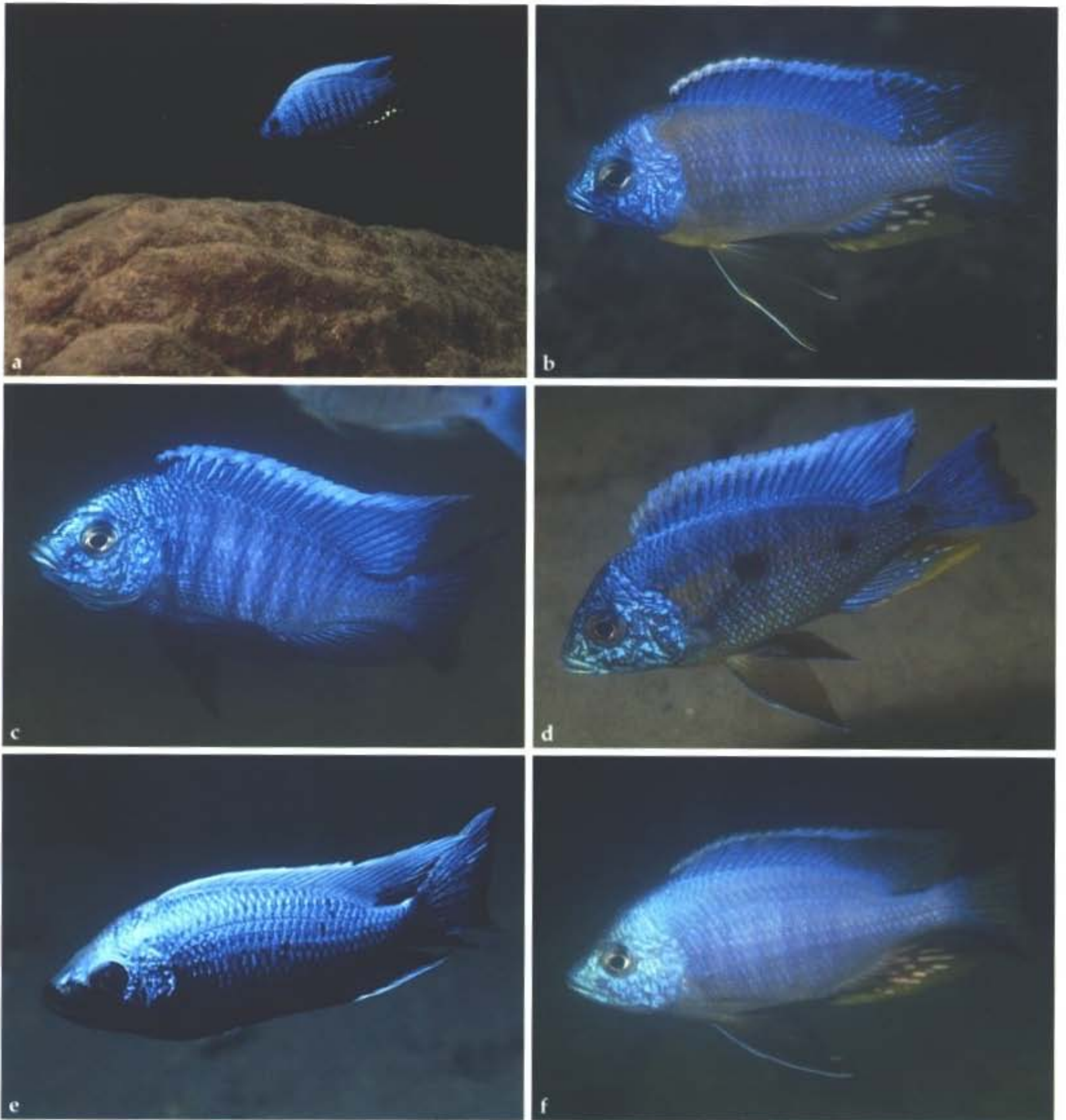


Fig. 2. **a**, *Copadichromis quadrimaculatus*, territorial male defending upper surface of a large boulder; Nkhungu Point, Mozambique. Note that male's breeding coloration obscures basic melanin pattern of lateral blotches. **b**, *C. mbenjii*, male in breeding coloration; Mbenji Island, Malawi. **c**, *C. azureus*, male in breeding coloration; Nkhomo Reef, Malawi. **d**, *C. verduyni*, male in breeding coloration; Narungu, Malawi. **e**, *C. trewavasae*, territorial male; Chizumulu Island, Malawi. **f**, *C. atripinnis*, male in breeding coloration; Thumbi West Island, Malawi.

vasae are known to occur along the Tanzanian shores, but none were included in this study.

Copadichromis trewavasae inhabits the sand/rock interface at depths of 15-25 m. Territorial males construct a bower by excavating sand or mud from beneath a rock and deposit it in front of the spawning cave forming a semi-circular elevated entrance. The slightly elevated rim of

the bower gives only a vague impression of a bowl. Spawning takes place underneath the rock. Females normally occur in small groups rarely numbering more than 10 individuals, and remain close to the bottom. Both males and females feed on plankton in the water column near the bottom and on benthic invertebrates.

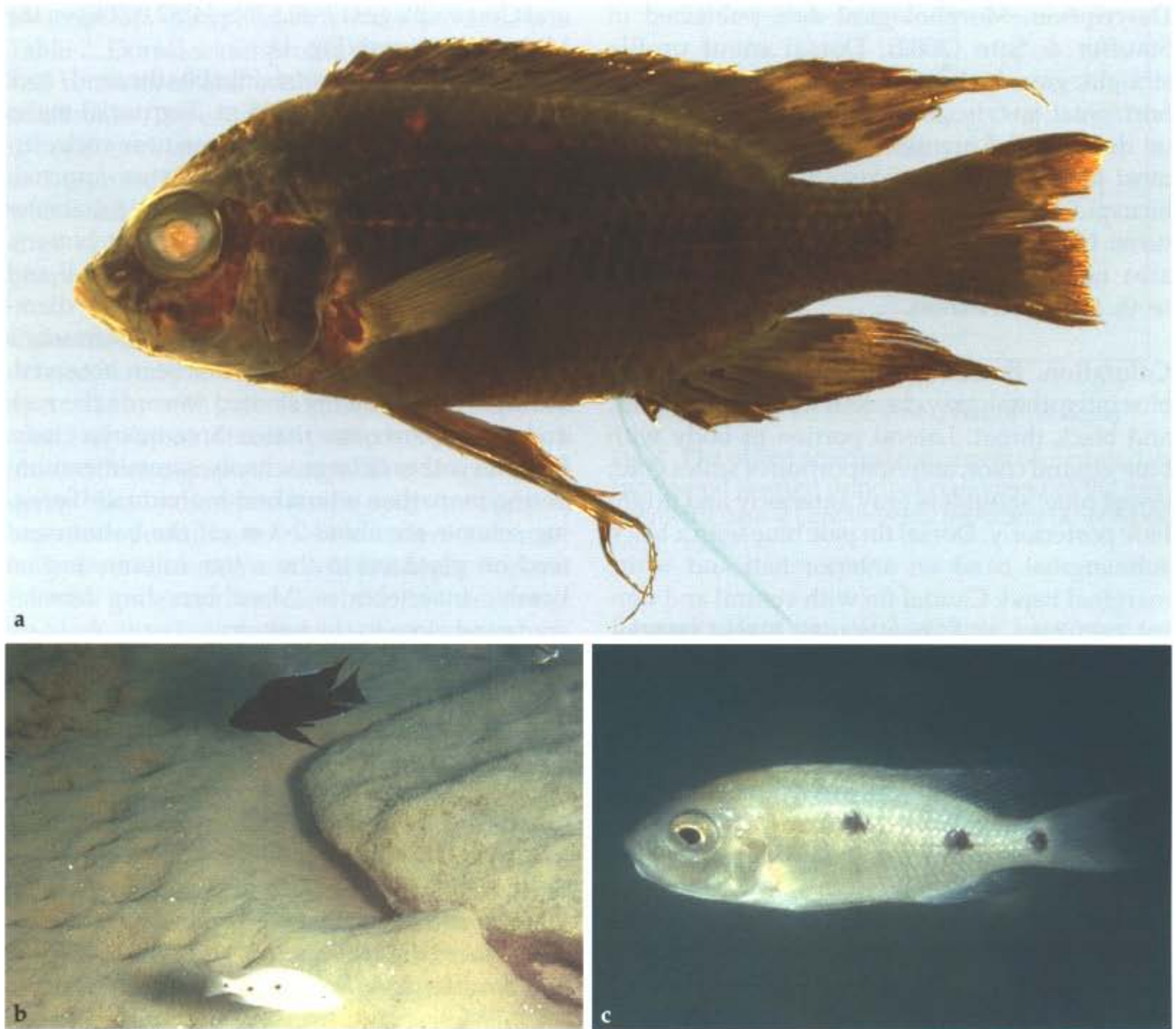


Fig. 3. *Copadichromis melas*; Mozambique: Lake Malawi, Mara Point; a, holotype, PSU 3635, 84.0 mm SL; b, bower; c, female, not preserved, approx. size 68 mm SL.

Copadichromis atripinnis Stauffer & Sato
(Fig. 2f)

Copadichromis atripinnis Stauffer & Sato, 2002: 92
(Malawi: Thumbi West Island: Kache Point).

Material examined. PSU 3387, holotype, 101.9 mm SL; PSU 3388, 33 paratypes; UMBC 002, 1 paratype, 66.9-103 mm SL; Malawi: Lake Malawi: Thumbi West Island: Kache Point, 14° 01.404'S 34° 49.439'E; E. Sato, 2 Apr. 1999. – PSU 3638, 19; UMBC 004, 1, 77.7-103.5 mm SL; Malawi: Lake Malawi: Gome Village, 13°30.744'S 34° 52.021'E; J. R. Stauffer & A. F. Konings, 12 Feb 2002.

Diagnosis. *Copadichromis atripinnis* is distinguished from other members of the *C. mbenjii* group by the possession of three lateral spots on the body (vs. two in *C. diplostigma* and one in

C. pleurostigma), a supra-pectoral spot that is about 1-1.5 times the supra-anal spot (vs. 2-2.5 times in *C. mbenjii* and *C. chizumuluensis*), and by a thin black submarginal band in the dorsal fin (vs. absent in *C. azureus*, *C. verduyni*, *C. trewavasae*, *C. insularis*, *C. cyanocephalus*, *C. parvus*, and *C. melas*). Breeding males are distinguished from those of the other species by the possession of a wide yellow marginal band in the anal fin (vs. narrow band in *C. azureus*, *C. trewavasae*, *C. chizumuluensis*, and *C. diplostigma*; vs. no band in *C. melas* and *C. parvus*), a blue breast (vs. yellow in *C. mbenjii*, *C. diplostigma*, and *C. verduyni* and black in *C. trewavasae* and *C. melas*), and a narrow black submarginal band in the dorsal fin (vs. no submarginal band in *C. insularis*, *C. cyanocephalus*, and *C. pleurostigma*).

Description. Morphological data published in Stauffer & Sato (2002). Dorsal snout profile straight; gape inclination of mouth about 35° to horizontal; jaws isognathous. Teeth in outer rows on dentary and premaxilla of mature males for most part large and unicuspid, with occasional bicuspid tooth; bicuspid in females and immatures. Lower pharyngeal jaw small, dentigerous area notched posteriorly, with small bicuspid teeth. Gill rakers short.

Coloration. Breeding males: head with bright blue interorbital, gray cheeks with blue highlights, and black throat. Lateral portion of body with blue ground color, anterior portion of scales gold; breast blue; shoulders gray anteriorly and bright blue posteriorly. Dorsal fin pale blue with a black submarginal band on anterior half and white marginal band. Caudal fin with ventral and dorsal two rays and membranes black; interior membranes transparent with blue rays and gold/yellow membranes. Anal-fin rays and membranes proximal three-fourths black; distal one-fourth with white membranes and yellow spines and rays. Pectoral fin clear. Proximal three-fourths of pelvic fin black; distal one-fourth clear, membranes with micro-melanophores; white leading edge.

Females: dorsal portion of head gray and ventral portion white; white throat. Lateral portion of body, dorsal one-third gray and ventral two-thirds white; anterior portion of scales outlined in gold; three conspicuous black spots on flank: supra-pectoral spot below 10-12th scale in contact with upper lateral line (Nankumba population) or not in contact with lateral line (Gome population) and about 1-1.5 times size of supra-anal spot; supra-anal spot at 22-24th scale above and in contact with lower lateral line and covering 3-4 scales; caudal spot on caudal base and onto peduncle. Three vertical bars between supra-pectoral spot and dorsal-fin origin. Dorsal fin clear with yellow spots, black submarginal band, white marginal band, and yellow lappets. Caudal-fin rays and membranes white with yellow spots. Proximal one-third of anal fin clear, middle one-third dusky, and distal one-third clear. Pectoral and pelvic fins clear.

Distribution and field observations. *Copadichromis atripinnis* occurs along the rocky shores of the Nankumba Peninsula and along those shores between the Masinje River (13°32.041'S 34°51.681'E)

and Gome Village (13°30.535'S 34°52.007'E) on the Malaŵi east coast (Fig. 1).

Copadichromis atripinnis inhabits the sand/rock interface at depths of 12-25 m. Territorial males construct bowers on sand slopes near rocky areas with distances between bowers approximately 2-7 m. The spawning bowl has a diameter of 26-42 cm and the rim is 3-9 cm off the bottom. The rock used in the construction is small and rarely wider than one third of the bowl's diameter (observations at Gome, Feb 2002). Excavations from beneath the rock have not been observed. The spawning bowl is slanted towards the rock and often spans more than a three-quarter circle. Females gather in large schools, sometimes numbering more than a hundred individuals. Foraging schools are about 2-3 m off the bottom and feed on plankton in the water column and on benthic invertebrates. Mouthbrooding females are found close to the bottom.

Copadichromis melas, new species

(Figs. 3, 7a)

Copadichromis sp. "midnight mloto", Konings, 2001: 318.

Holotype. PSU 3635, 84 mm SL; Mozambique: Lake Malaŵi: Mara Point, 12°11.254'S 34°41.968'E; J. R. Stauffer & A. F. Konings, 16 Feb 2002.

Paratypes. PSU 3636, 14; UMBC 003, 1, 58.0-88.5 mm SL; data as for holotype.

Diagnosis. *Copadichromis melas* is distinguished from the other members of the *C. mbenjii* group by the possession of three lateral spots on the body (vs. two in *C. diplostigma* and one in *C. pleurostigma*) and a supra-pectoral spot that is about the same size as the supra-anal spot (vs. 2-2.5 times in *C. mbenjii* and *C. chizumuluensis* and about 1.5 times in the other species except *C. cyanocephalus*, *C. atripinnis* and *C. parvus*). It is distinguished from *C. parvus* and *C. cyanocephalus* by three vertical bars between the supra-pectoral spot and the opercle (vs. two). It is distinguished from *C. atripinnis* by the lack of a black submarginal band in the dorsal fin. Breeding males of *C. melas* are entirely black and have a black anal fin without colored margin, spots, or streaks and is thus distinguished from males of all other species in the *C. mbenjii* group.

Description. Morphometric and meristic data in Table 2. Dorsal snout profile straight in females and immatures and with a slight concavity in adult males; gape inclination of mouth about 40° to horizontal; jaws isognathous. Teeth on dentary and premaxilla in three rows; outer row teeth with small bicuspid teeth in juveniles and females; large unicuspid teeth in mature males. Lower pharyngeal jaw not examined. Gill rakers short.

Coloration. Breeding males: interorbital portion of head black; preorbital, cheek, opercle, and preopercle gray with green highlights; black opercle spot and throat. Lateral portion of body, dark blue with orange posterior outline of scales and seven black bars; three lateral spots on body of captured specimens not visible underwater; gray belly. Dorsal, caudal, and anal fins black. Pectoral fin with gray rays and clear membranes. Pelvic fin black anteriorly fading to gray posteriorly.

Females: head brown/gray; cheek white with green highlights; opercle white with blue highlights; throat white. Lateral portion of body, gray dorsally fading to white ventrally with blue and purple highlights; three black spots: supra-pectoral spot below 10-13th scale separate from upper lateral line and about same size as supra-anal spot; supra-anal spot at 23-24th scale above and in contact with lower lateral line and covering 3-4 scales; caudal spot on caudal base. Three vertical bars between supra-pectoral spot and dorsal-fin origin. Dorsal fin clear with faint orange/brown spots and pale yellow lappets. Caudal fin light gray. Anal fin clear with orange/brown tints. Pectoral and pelvic fins clear.

Distribution and field observations. *Copadichromis melas* occurs in the sand/rock interface along the Mozambique shore of the lake between Tumbi Point (Fig. 1; 12°20.935'S 34°41.966'E) and Cobwé (Fig. 1; 12°08.064'S 34°45.554'E). At the latter locality, it occurs sympatrically with *C. trewavasae*.

Territorial males build their bowers at depths of 10-15 m. The bowers are excavated under rocks that are often larger than the bower diameter. They have elevated rims. The rim is normally much higher at the point of contact with the rock than in the center of the entrance. The width of the spawning cave under the rock is 7-24 cm and the entrance height 3-6.5 cm. Females are commonly solitary or in small groups of 3-4 individuals. Both males and females feed on plankton near the bottom and on benthic invertebrates.

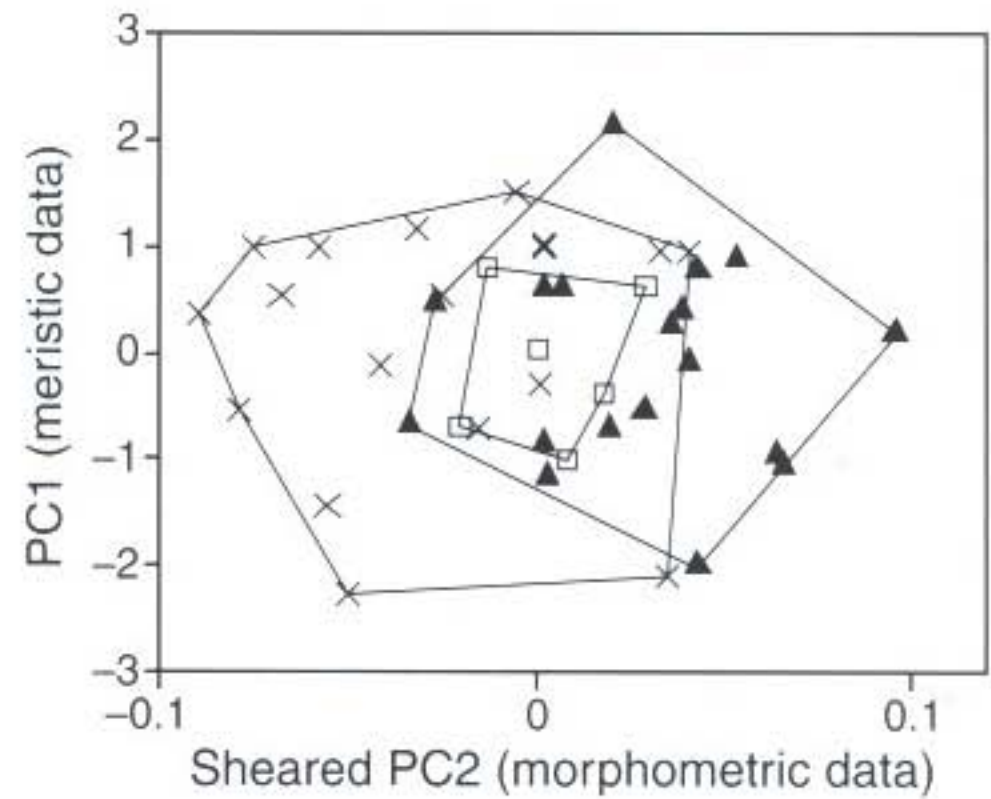


Fig. 4. Plot of first principal component of meristic data and second sheared principal component of the morphometric data of *Copadichromis trewavasae* (▲; □: types) and *C. melas* (×).

Remarks. In a statistical analysis, we compared six paratypes of *C. trewavasae* collected from Likoma Island (Konings, 1999) and 18 individuals of *C. trewavasae* that we collected from Membe Island (Chizumulu) with the 16 types of *C. melas* (Fig. 4). When the first principal components of the meristic data were plotted against the second sheared principal components of the morphometric data of the *C. trewavasae* collected from Chizumulu Island and Membe Island the minimum polygon clusters formed were not significantly different ($p > 0.05$, MANOVA). The cluster formed by the data of *C. melas* largely overlaps with those of the two *C. trewavasae* populations, but in a MANOVA test it is significantly different ($p < 0.05$) from the two clusters formed by *C. trewavasae*. We were unable, however, to find a single morphometric or meristic character, which did not overlap among the three populations. Variables that had the highest loading on second principal components of the morphometric data were cheek depth (-0.74) and caudal peduncle length (0.49); while those with the highest loadings on the principal components of the meristic data were dorsal-fin rays (-0.629), dorsal-fin spines (0.587), and post lateral-line scales (0.384). Males in breeding colors are easily distinguished and at Cobwé, Mozambique, both species occur sympatrically and mate assortatively (observations Feb 2002; Nov 2003); thus, demonstrating that they are, in fact, distinct species.

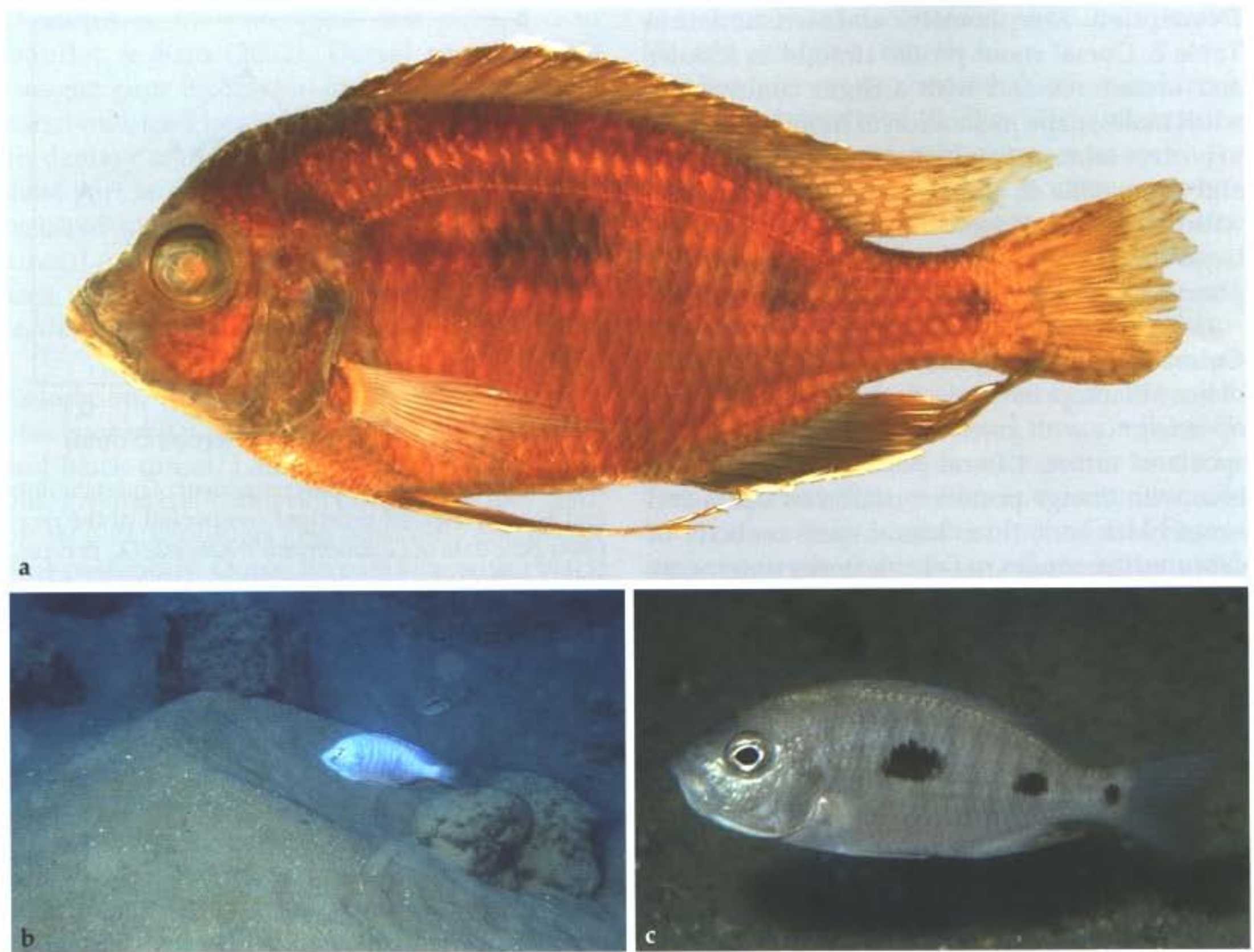


Fig. 5. *Copadichromis chizumuluensis*; Malaŵi: Lake Malaŵi, Chizumulu Island; **a**, holotype, PSU 3644, 106.4 mm SL; **b**, territorial male at bower; **c**, female, not preserved, approx. size 90 mm SL.

Etymology. From the Greek adjective *melas* (black) to denote the entirely black coloration of breeding males.

Copadichromis chizumuluensis, new species
(Figs. 5, 7b)

Copadichromis sp. “chizumulu blue”, Konings, 2001: 319.

Holotype. PSU 3644, 106.4 mm SL; Malaŵi: Chizumulu Island: Mkanila Bay, 12°00.566'S 34°36.828'E; J. R. Stauffer & A. F. Konings, 19 Feb 2002.

Paratypes. PSU 3645, 16; UMBC 007, 1, 77.4-105.9 mm SL; data as for holotype.

Diagnosis. *Copadichromis chizumuluensis* is distinguished from the other members of the *C. mbenjii* group by a supra-pectoral spot that is 2-2.5 times the diameter of the supra-anal spot (vs. 1-1.5 times in all other members of this group except *C. pleurostigma* and *C. diplostigma*, which lack a supra-anal spot, and *C. mbenjii*). It is distinguished from *C. mbenjii* by the possession of 17-19 gill rakers on the first ceratobranchial (vs. 12-15 in *C. mbenjii*). Male *C. chizumuluensis* in breeding coloration are distinguished from those of the *C. mbenjii* group by a blue breast (vs. yellow in *C. mbenjii*, *C. verduyni*, and *C. diplostigma*; vs. black in *C. melas* and *C. trewavasae*) and by a narrow yellow marginal band in the anal fin (vs. wide yellow band in *C. atripinnis*, *C. cyanocephalus*, *C. chizumuluensis*, *C. insularis*, and *C. pleurostigma*; vs. no colored margin in *C. melas* and *C. parvus*). Males are distinguished from those of *C. azureus* by light spots in the anal fin (vs. no spots or streaks in anal).



Fig. 6. *Copadichromis diplostigma*; **a**, holotype, PSU 3654, 112.2 mm SL; Malawi, Likoma Island, Maingano Island; **b**, bower at Ndumbi Rocks, Likoma; **c**, female, not preserved, approx. size 80 mm SL; Likoma Island, Ndomo Point.

Description. Morphometric and meristic data in Table 2. A small plankton-feeding cichlid (Figs. 5, 7b) with deep body and straight, in females and immatures, to concave, in large adults, dorsal head profile; gape inclination of mouth about 40° to horizontal; jaws isognathous. Teeth on dentary and premaxilla in three rows; teeth in outer row bicuspid in juveniles and females; teeth in outer row of mature males large and unicuspid. Lower pharyngeal jaw small, dentigerous area slender, with tiny bicuspid teeth and posterior row enlarged with two central teeth about $2\times$ width of others. Gill-rakers on ceratobranchial short and broad-based with lower 6-8 reduced to short stubs.

Coloration. Breeding males: head blue with green highlights; preorbital region gray; throat white with gray patches. Lateral portion of body, blue, with anterior portion of scales above upper

lateral line orange/brown and anterior portion of scales below upper lateral line gold. Breast gray with blue spots; belly gray with blue/white highlights. Dorsal membranes pale yellow with blue markings; membranes between rays with yellow spots; spines and rays blue proximally and gray distally; black marginal band with white lappets and yellow tips. Caudal fin with blue rays and blue and yellow membranes; black band located two-thirds distally. Proximal two-thirds of anal fin with small blue ocelli; margin black band with yellow lappets. Pectoral fin clear. Pelvic fin clear with white leading edge and black band located two-thirds distally.

Females: head gray; cheeks silvery with purple highlights; opercle silver with brown and blue highlights and black opercle spot. Throat white. Lateral portion of body with three black spots: supra-pectoral spot below 9-14th scale sometimes in contact with upper lateral line and about 2-2.5

times size of supra-anal spot; supra-anal spot at 23-25th scale above and in contact with lower lateral line and covering 3-4 scales; caudal spot smaller than supra-anal spot on caudal base ex-

tending onto caudal peduncle; above upper lateral line bronze ground color with green highlights; below upper lateral line silver ground color with center of each scale either blue or yellow

Table 2. Morphometric and meristic values of *Copadichromis melas*, *C. chizumuluensis*, and *C. diplostigma*. Range includes holotype. H, holotype.

	<i>C. melas</i> Mara Point, Mozambique (n = 16)		<i>C. chizumuluensis</i> Mkanila Bay, Chizumulu, Malawi (n = 17)		<i>C. diplostigma</i> Maingano Island, Likoma, Malawi (n = 20)	
	H	range	H	range	H	range
Standard length, mm	84	58.0-88.5	106.4	77.4-106.4	112.2	76.8-112.2
Head length, mm	27	18.6-28.5	32.6	22.4-32.6	31.7	22.7-31.7
Percent standard length						
Head length	32.1	30.5-33.3	30.6	29.1-33.2	28.3	28.0-32.0
Body depth	34.9	32.3-37.0	38.9	35.1-41.1	33.3	33.1-37.3
Snout to dorsal-fin	36.4	32.9-37.8	35.3	32.8-36.8	32	31.3-35.4
Snout to pelvic-fin	39.4	36.4-43.2	37.5	35.3-41.8	34.6	34.4-38.9
Dorsal-fin base length	57.8	53.5-60.9	59.6	56.2-61.7	58.1	56.0-61.3
Anterior dorsal to anterior anal	52.6	48.4-56.5	55.7	51.6-55.7	50.6	47.1-54.3
Anterior dorsal to posterior anal	60.9	56.8-62.2	64.8	60.3-65.1	62.2	59.4-64.7
Posterior dorsal to anterior anal	32.8	29.0-35.7	33.9	31.5-37.5	32	31.4-36.1
Posterior dorsal to posterior anal	16.2	14.3-17.5	16.3	14.9-16.9	14.8	14.7-17.1
Posterior dorsal to ventral caudal	17.8	17.7-20.8	19.4	18.0-21.2	19.9	17.4-21.0
Posterior anal to dorsal caudal	21.8	20.8-23.7	22	19.2-23.4	22.7	20.4-25.1
Anterior dorsal to pelvic-fin origin	37.7	34.7-39.9	41.1	37.2-43.7	36.8	33.3-38.9
Posterior dorsal to pelvic-fin origin	55.6	53.6-58.7	60	58.3-61.7	59.9	54.8-60.9
Caudal peduncle length	15.1	15.9-18.5	15.5	14.8-18.9	18.5	16.0-19.5
Least caudal peduncle depth	11.4	10.7-13.1	12.1	11.1-13.7	11.2	10.2-12.2
Percent head length						
Snout length	29.4	28.3-31.4	31.7	27.4-34.1	31.4	27.7-35.2
Postorbital head length	36.5	33.3-38.1	36.7	34.8-39.6	38.6	35.5-39.9
Horizontal eye diameter	36.4	34.1-42.4	31.8	31.8-40.7	35.7	32.4-38.4
Vertical eye diameter	35.6	33.2-41.9	32.1	32.1-40.3	33.4	30.6-39.8
Head depth	97.3	85.4-102.0	109.8	99.0-112.5	105.9	98.8-116.3
Preorbital depth	17.3	12.1-18.9	19.4	14.8-20.2	18.5	14.4-19.9
Cheek depth	22.6	16.9-24.2	24.1	19.4-27.4	23.7	16.7-25.9
Lower jaw length	34.7	32.5-39.9	36.2	36.2-45.1	39.5	34.9-41.7
Counts						
Dorsal-fin spines	15	15-17	17	16-17	16	16-17
Dorsal-fin rays	12	10-12	11	11-12	12	11-13
Anal-fin spines	3	3	3	3	3	3
Anal-fin rays	8	8-9	10	9-10	10	9-10
Pelvic-fin rays	5	5	5	5	5	5
Pectoral-fin rays	13	12-13	13	12-14	14	13-15
Lateral line scales	32	30-33	34	33-35	34	33-35
Pored scales posterior to lateral line	1	1-3	2	1-3	2	1-2
Scale rows on cheek	3	2-3	2	2-3	3	2-3
Gill rakers 1 st ceratobranchial	15	14-19	18	17-19	16	13-19
Gill rakers 1 st epibranchial	5	5-6	6	6-7	6	5-8
Teeth outer left lower jaw	12	10-14	16	14-19	12	12-16
Teeth rows upper jaw	3	3	3	3	3	3
Teeth rows lower jaw	3	3	3	3	3	3-4

and anteriorly outlined in gold. Two to three vertical bars between supra-pectoral spot and dorsal-fin origin. Breast and belly white. Dorsal fin dark gray with orange spots, white lappets, and yellow tips. Proximal one-third of caudal fin dark gray, distal two-thirds light gray with yellow spots. Proximal two-thirds of anal fin dark gray, distal one-third light gray with yellow ocelli. Pectoral fin clear. First two membranes and rays of pelvic fin gray, remaining clear.

Distribution and field observations. *Copadichromis chizumuluensis* is endemic to Chizumulu Island (Fig. 1).

Males build bowers in the sand/rock interface at depths of 12-20 m. The spawning site is not always beneath a rock and can also be alongside a rock. On sandy bottoms, a male can bank sand to 30 cm high. Such a bower resembles more of a sand turret than a bowl, and spawning takes place between the rock and the sand mound. On flocculent substrates, males often excavate from beneath a rock and have much shallower bowers. Bowes have a diameter of 26-37 cm and the entrance to a spawning cave under the rock can be 13 cm high. Females occur in small groups and feed, like males, on plankton in the water column and on benthic invertebrates.

Etymology. The specific epithet, an adjective, refers to Chizumulu Island to which this species is endemic.

Copadichromis diplostigma, new species
(Figs. 6, 7c)

Copadichromis sp. "likoma blue", Konings, 2001: 319.

Holotype. PSU 3654, 112.2 mm SL; Malaŵi: Likoma Island: Maingano Island, 12°02.818'S 34°45.547'E; J. R. Stauffer & A. F. Konings, 18 Feb 2002.

Paratypes. PSU 3655, 18; UMBC 10, 1, 76.8-110.4 mm SL; data as for holotype.

Diagnosis. Two lateral spots (supra-pectoral and caudal) on body distinguish *C. diplostigma* from all other species of the *C. mbenjii* group. Breeding males are distinguished from those of most other species in the *C. mbenjii* group by a yellow breast

(vs. blue in *C. azureus*, *C. atripinnis*, *C. chizumuluensis*, *C. insularis*, *C. cyanocephalus*, *C. parvus*, and *C. pleurostigma* or black in *C. trewavasae* and *C. melas*) and from *C. mbenjii* and *C. verduyni* by a narrow yellow marginal band on the anal fin (vs. a wide yellow band).

Description. Morphometric and meristic data in Table 2. A small plankton-feeding cichlid (Figs. 6, 7c) with dorsal snout profile straight in females and immatures, slightly concave in adult males; gape inclination of mouth about 40° to horizontal; jaws isognathous. Teeth on dentary and premaxilla in 3-4 rows; outer row with bicuspid teeth in juveniles and females; some large unicuspid teeth in outer row of mature males. Lower pharyngeal jaw thin and set with minute bicuspid teeth; posterior row with enlarged teeth; no wider teeth in the center. Gill rakes small but not widened at the base.

Coloration. Breeding males: head with gray interorbital, green preorbital, blue cheek with green highlights, gray opercle with blue opercle spot, and yellow throat. Lateral portion of body, blue with green highlights dorsally, gray with yellow highlights ventrally. Posterior portions of scales blue. Yellow breast and white belly. Dorsal fin blue proximally, gray distally with yellow spots; black submarginal band with white marginal band and yellow lappets. Dorsal and ventral rays of caudal fin black; middle rays blue with yellow membranes. Anal fin with narrow yellow marginal band; rays black with purple membranes. Pectoral fin clear. Pelvic fin with white leading edge and first two rays and membranes black; remaining rays and membranes clear.

Females: head gray with white cheek and throat. Lateral portion of body gray dorsally, fading to white ventrally; posterior portion of scales blue and anterior portion pale yellow. Lateral portion of body with two black spots: supra-pectoral spot not in contact with upper lateral line and below 8-12th scale and about 5 times diameter of caudal spot; caudal spot on caudal base. Three vertical bars between supra-pectoral spot and dorsal-fin origin. Dorsal fin clear with yellow spots and yellow tips. Caudal fin clear with some orange spots proximally; anal fin clear with yellow patches. First two membranes of pelvic fin yellow, remainder clear. Pectoral fin clear.



Fig. 7. **a**, *Copadichromis melas*, breeding male, not preserved, approx. size 85 mm SL; Mozambique: Mara Point; **b**, *C. chizumuluensis*, breeding male, not preserved, approx. size 100 mm SL; Malawi, Chizumulu Island; **c**, *C. diplostigma*, breeding male, not preserved, approx. size 100 mm SL; Malawi: Likoma, Ndumbi Rocks.

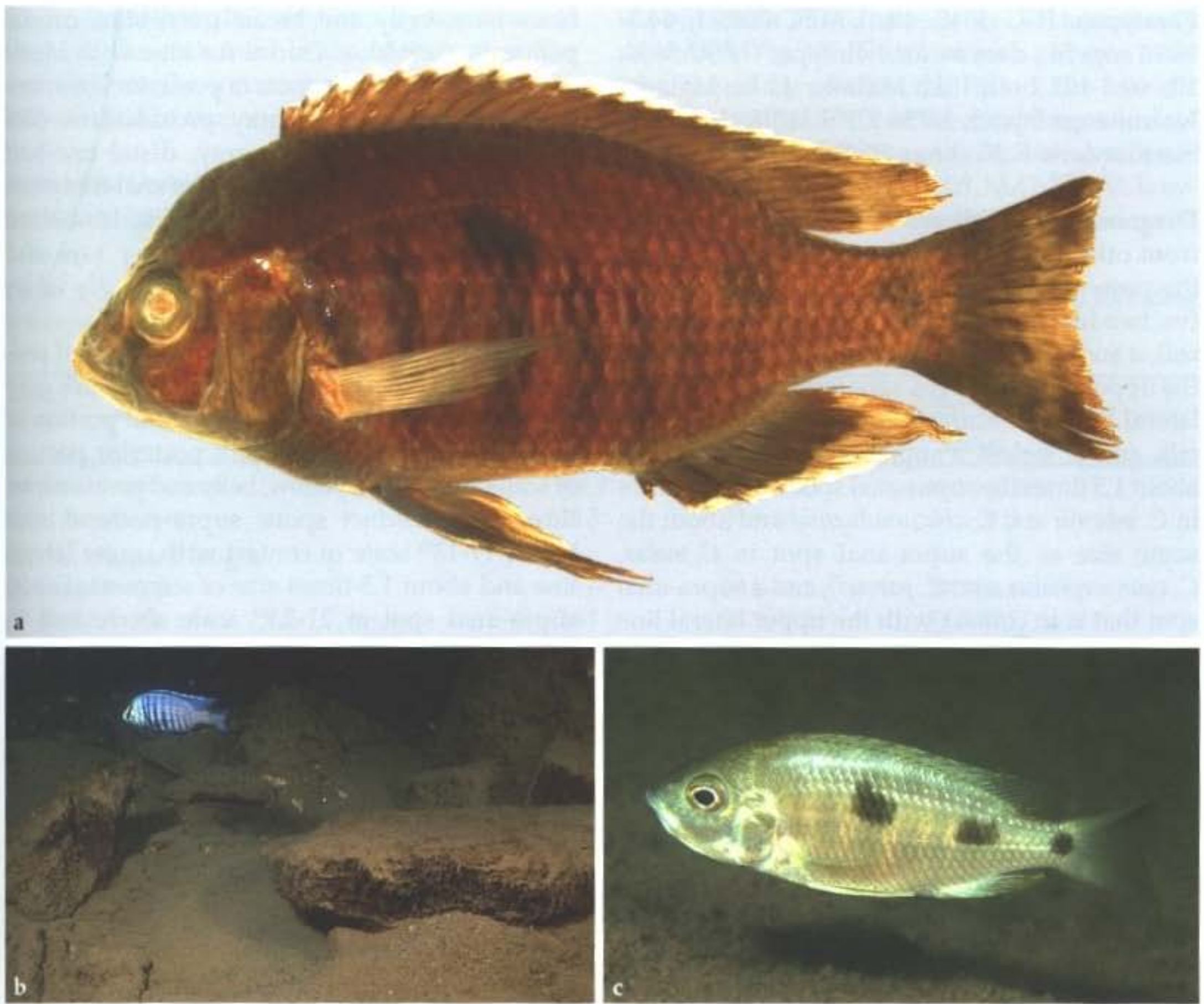


Fig. 8. *Copadichromis insularis*; **a**, holotype, PSU 3646, 109.3 mm SL; Malawi: Lake Malawi, Chinyankwazi Island; **b**, bower at Nakantenga Island, Malawi; **c**, female, not preserved, approx. size 85 mm SL; Malawi: Chinyankwazi Island.

Distribution and field observations. *Copadichromis diplostigma* occurs around Likoma Island but similar forms have been observed, but not included in this study, near Cobwe in Mozambique and near Undu in Tanzania (Fig. 1).

Territorial males *C. diplostigma* construct bowers at the sand/rock interface at depths of 12-18 m. On bottoms with fine sand, the bower consists of a bowl with a high wall opposite the rock and a slanted spawning platform. Males carry sand from the environment to build their bowers because its shape demands much more material than can be recovered from beneath the rock. On muddy bottoms or those with coarse substrates, males defend much shallower bowers. On average, a bower has a diameter of approximately 20 cm and the height of the outer edge varies between 3-10 cm. Females and immature males

occur in small groups and feed on plankton in the water column and on benthic invertebrates.

Etymology. From the Greek diplo (double) and Latin stigma (spot) referring to the two lateral spots on the body of this species. A noun in apposition.

Copadichromis insularis, new species
(Figs. 8, 12a)

Copadichromis azureus (part) Konings, 1990: 112; 2001: 318.

Holotype. PSU 3646, 109.3 mm SL; Malawi: Lake Malawi: Chinyankwazi Island, 13°50.351'S 34°57.376'E; J. R. Stauffer & A. F. Konings, 26 Feb 2002.

Paratypes. PSU 3647, 14; UMBC 008, 1, 64.3-110.4 mm SL; data as for holotype. – PSU 3650, 13, 69.3-102.2 mm SL; Malawi: Lake Malawi: Nakantenga Island, 13°54.925'S 34°38.618'E; J. R. Stauffer & A. F. Konings, 22 Feb 2002.

Diagnosis. *Copadichromis insularis* is distinguished from other members of the *C. mbenjii* group by the possession of three lateral spots on the body (vs. two in *C. diplostigma* and one in *C. pleurostigma*), a supra-pectoral spot that is in contact with the upper lateral line (vs. separate from the upper lateral line in *C. azureus*, *C. cyanocephalus*, *C. parvus*, and *C. melas*), a supra-pectoral spot that is about 1.5 times the supra-anal spot (vs. 2-2.5 times in *C. mbenjii* and *C. chizumuluensis* and about the same size as the supra-anal spot in *C. melas*, *C. cyanocephalus*, and *C. parvus*), and a supra-anal spot that is in contact with the upper lateral line (vs. separate from the upper lateral line in *C. trewavasae*, *C. atripinnis*, and *C. verduyni*). Breeding males are distinguished from those of the other species by the possession of a wide yellow marginal band in the anal fin (vs. narrow band in *C. azureus*, *C. trewavasae*, *C. chizumuluensis*, and *C. diplostigma*; vs. no band in *C. melas* and *C. parvus*), a blue breast (vs. yellow in *C. mbenjii*, *C. diplostigma*, and *C. verduyni*; vs. black in *C. trewavasae* and *C. melas*), by the lack of a black submarginal band in the dorsal (vs. submarginal band in *C. atripinnis*), and by a white margin of the dorsal fin (vs. yellow in *C. cyanocephalus* and *C. pleurostigma*).

Description. Morphometric and meristic data in Table 3. Small cichlid (Figs. 8, 12a) with dorsal snout profile straight to slightly concave in large males; gape inclination of mouth about 45° to horizontal; jaws isognathous. Teeth on dentary and premaxilla in 3-4 rows; outer row with small bicuspid teeth in juveniles and females; large unicuspid teeth in mature males. Lower pharyngeal jaw with small bicuspid teeth; posterior row with slightly enlarged teeth. Gill rakers short and broad-based.

Coloration. Breeding males: head dark blue/gray with blue interorbital bars; cheek and opercle with yellow green and light blue highlights; gray opercle spot and throat; black subocular bar observed in specimens underwater; bar invisible almost immediately when specimens removed from lake. Lateral portion of body, blue with six

black bars; belly and breast gray/blue; caudal peduncle dark blue. Dorsal fin blue with blue/white lappets; orange spots in posterior 2-6 membranes. Caudal-fin rays gray; proximal one-half of caudal-fin membranes gray, distal one-half blue/white. Proximal two-thirds of anal-fin spines and membranes black/dark gray; distal one-third yellow/white. Pectoral fin with gray rays and clear membranes. Pelvic fin black with white leading edge.

Females: head gray; cheek, opercle, and preopercle with blue and green highlights; dark gray opercle spot and white throat. Lateral portion of body, blue ground color with posterior portion of scales outlined in yellow; belly and breast white; three very distinct spots: supra-pectoral spot below 11-13th scale in contact with upper lateral line and about 1.5 times size of supra-anal spot; supra-anal spot at 21-23rd scale above and in contact with upper and lower lateral line and covering about 3 scales; caudal spot about same diameter as supra-anal spot on caudal base and extending onto peduncle; three vertical bars between supra-pectoral spot and dorsal-fin origin. Dorsal fin blue/white with tips of posterior five rays orange/brown. Caudal fin with gray rays and blue membranes. Anal fin with gray rays and blue membranes and four yellow ocelli. Pectoral fin clear. First ray and membrane of pelvic fin black with white leading edge; remaining portion clear.

Distribution and field observations. *Copadichromis insularis* inhabits the sand/rock interface of the Maleri islands (Fig. 1) at depths of 13-18 m and over sandy patches around Chinyankwazi and Chinyamwezi islets (Fig. 1) at depths similar to that of the Maleri populations. The Maleri islands are some 35 km from Chinyankwazi and Chinyamwezi islands; thus, other populations of *C. insularis* may be found at intermediate locales.

Females and non-territorial males gather in small schools (up to 10 individuals) and feed on plankton in the water column 1-3 m above the bottom. Territorial males usually excavate their spawning bowl from beneath flat rocks. Such rocks are normally larger than the diameter of the bowl. The diameter of the bower is 22-34 cm and the height of the 'spawning cave' 3-10 cm. The bowl in front of the rock spans just about a half-circle or a little less. Spawning takes place underneath the rock. The bower of *C. insularis*

differs from that of *C. atripinnis* by the size and shape of the rock used in the construction (flat and large in the former and small and irregularly shaped in the latter).

Remarks. *Copadichromis insularis* was initially thought to be a geographical variant of *C. atripin-*

nis, but in our PCA analyses the two taxa clearly separated (Fig. 10). The minimum polygon clusters formed by plotting the PC1 of the meristic data against the SPC2 of the morphometric data for the two populations of *C. insularis* were not significantly different ($p > 0.05$, MANOVA); however, the two clusters formed by *C. insularis* were

Table 3. Morphometric and meristic values of *Copadichromis insularis* from Chinyankwazi (n=16, including holotype) and Nakantenga (n=13) islands, Malaŵi. Range includes holotype.

	Chinyankwazi		Nakantenga
	holotype	range	range
Standard length, mm	109.3	64.3-110.4	69.3-102.2
Head length, mm	33.5	20.5-34.7	23.3-31.3
Percent standard length			
Head length	30.6	29.1-32.5	29.7-33.6
Body depth	36.1	33.9-37.2	34.8-37.7
Snout to dorsal-fin	34.3	32.5-35.7	33.6-37.6
Snout to pelvic-fin	38.8	35.9-42.0	34.0-41.1
Dorsal-fin base length	60.7	56.3-60.7	55.6-59.9
Anterior dorsal to anterior anal	55.3	49.1-55.3	50.0-55.1
Anterior dorsal to posterior anal	64.6	59.2-64.6	59.7-63.6
Posterior dorsal to anterior anal	34.1	30.9-34.7	31.0-34.8
Posterior dorsal to posterior anal	17.8	15.6-18.6	15.8-17.4
Posterior dorsal to ventral caudal	20.3	18.2-21.4	18.4-21.2
Posterior anal to dorsal caudal	24.8	20.4-24.8	21.2-24.2
Anterior dorsal to pelvic-fin origin	41.2	33.7-41.2	37.0-39.3
Posterior dorsal to pelvic-fin origin	56.7	54.1-59.8	56.0-60.0
Caudal peduncle length	18.2	16.1-18.9	15.1-18.7
Least caudal peduncle depth	13.3	11.3-13.4	11.6-13.0
Percent head length			
Snout length	32.4	27.6-35.1	28.0-31.9
Postorbital head length	40.6	34.9-40.7	35.6-41.4
Horizontal eye diameter	31	30.3-37.8	32.6-36.9
Vertical eye diameter	31.3	28.6-35.4	31.6-37.8
Head depth	107.9	89.4-108.1	97.2-104.9
Preorbital depth	20.7	14.8-21.0	17.0-20.5
Cheek depth	22.8	17.1-24.9	20.2-25.4
Lower jaw length	36.3	33.8-42.0	33.4-39.3
Counts			
Dorsal-fin spines	17	15-17	16-17
Dorsal-fin rays	10	10-11	10-11
Anal-fin spines	3	3	3
Anal-fin rays	8	8-9	8-9
Pelvic-fin rays	5	5	5
Pectoral-fin rays	12	12-14	13-14
Lateral line scales	33	32-34	32-34
Pored scales posterior to lateral line	2	1-3	1-2
Scale rows on cheek	2	2-3	2
Gill rakers 1 st ceratobranchial	12	12-16	13-16
Gill rakers 1 st epibranchial	5	4-5	4-6
Teeth outer left lower jaw	11	10-14	11-14
Teeth rows upper jaw	3	3-4	3-4
Teeth rows lower jaw	3	3-4	3



Fig. 9. *Copadichromis cyanocephalus*, Mozambique: Lake Malaŵi, Charley's Bay; a, holotype, PSU 3639, 90.2 mm SL; b, bower; c, PSU 3643, female, paratype, 76 mm SL.

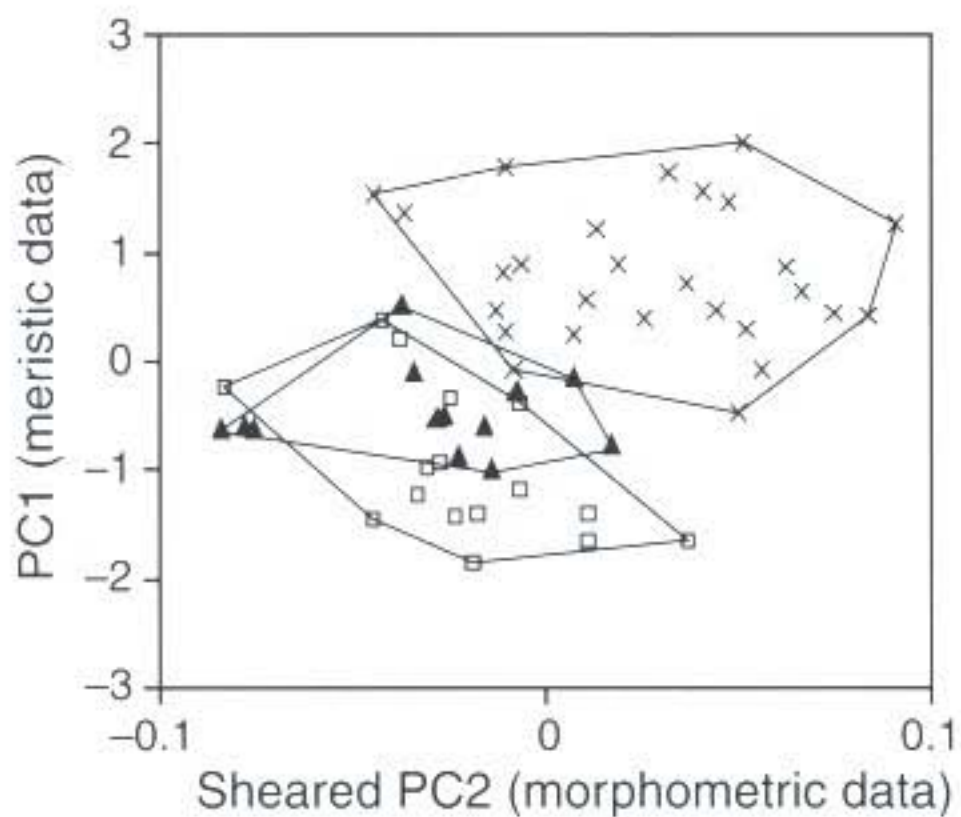


Fig. 10. Plot of first principal component of meristic data and second sheared principal component of the morphometric data of *Copadichromis insularis* (□: Chiny.; ▲: Nak.) from Chinyankwazi Island and Nakantenga Island and *C. atripinnis* (×).

significantly different from that formed by *C. atripinnis* along both axes ($p < 0.05$, ANOVA). Variables that had the highest loading on second principal components of the morphometric data were preorbital depth (-0.46), cheek depth (-0.411), and snout length (-0.403); while those with the highest loadings on the principal components of the meristic data were anal-fin rays (0.255), dorsal-fin rays (0.225), and gill rakers on the first ceratobranchial (0.227).

When comparing the shape of the bowers of either species, we noticed that those of *C. insularis* normally include a flat rock or slab, which is larger than the bower's diameter. Those of *C. atripinnis* normally have smaller rocks that have an irregular shape, and the outer rim of the spawning bowl is usually higher off the bottom than that of *C. insularis*. Morphologically there are some



Fig. 11. **a**, *Copadichromis parvus*, holotype, PSU 3648, 87.2 mm SL; Mozambique: Lake Malaŵi, Lumessi; **b**, Bower of *C. parvus* at Chilolo, Mozambique; **c**, *C. parvus*, female, not preserved, approx. size 70 mm SL; Mozambique, Chilolo.

minor differences in the head profile which shows a slightly more produced snout in *C. insularis* compared to the straight snout profile of *C. atripinnis*.

Etymology. From the Latin adjective *insularis* (of islands). It refers to the fact that the known populations all occur at islands.

Copadichromis cyanocephalus, new species
(Figs. 9, 12b)

Copadichromis sp. “verduyni blueface”, Konings 2001: 315.

Holotype. PSU 3639, 90.2 mm SL; Mozambique: Lake Malaŵi: Charley’s Bay, 13°22.262’S 34°50.075’E; J. R. Stauffer & A. F. Konings, 13 Feb 2002.

Paratypes. PSU 3640, 18; UMBC 006, 1, 66.3–87.8 mm SL; data as for holotype.

Diagnosis. *Copadichromis cyanocephalus* is distinguished from the other species of the *C. mbenjii* group by the possession of three lateral spots on the body (vs. two in *C. diplostigma* and one in *C. pleurostigma*) and a supra-pectoral spot that is about the same size as the supra-anal spot (vs. 2–2.5 times in *C. mbenjii* and *C. chizumuluensis* and about 1.5 times in the other species except *C. melas*, *C. atripinnis* and *C. parvus*). It is distinguished from *C. melas* by two vertical bars between the supra-pectoral spot and the opercle (vs. three). It is distinguished from *C. atripinnis* by the lack of a black submarginal band in the dorsal fin. Male *C. cyanocephalus* in breeding coloration are distinguished from those of other species in the *C. mbenjii* group by a blue breast (vs. yellow in *C. mben-*

jii, *C. diplostigma*, and *C. verduyni* or black in *C. trewavasae* and *C. melas*) and by a narrow yellow marginal band in the anal fin (vs. a wide band in *C. atripinnis*, *C. pleurostigma*, *C. cyanocephalus*, and *C. insularis* or no band in *C. parvus*). Males are distinguished from those of *C. chizumuluensis* by the lack of any spots or streaks in the anal fin.

Description. Morphometric and meristic data in Table 4. A small plankton-feeding cichlid (Figs. 9, 12b) with dorsal snout profile straight to slightly concave in large males; gape inclination of mouth 30-35° to horizontal; jaws isognathous. Teeth on dentary and premaxilla in three rows; outer row with small bicuspid teeth in juveniles and females; large unicuspid teeth in mature males. Pharyngeal jaws not examined. Gill rakers short and broad-based.

Coloration. Breeding males: head blue with green highlights; interorbital dark gray with blue highlights; blue and green opercle; posterior portion of throat green, anterior portion light green. Lateral portion of body, dark blue ground color dorsally, fading to blue/green ventrally; seven dark gray bars. Breast and belly blue with orange markings. Dorsal fin blue with green and purple highlights; yellow/white marginal band with yellow/orange lappets. Caudal fin with black rays and gray membranes. Anal fin blue/gray proximally, yellow/orange distally. Pectoral fin with black rays and clear membranes. Pelvic fin with black rays and gray membranes.

Females: head gray dorsally, fading to white ventrally; purple and silver highlights on cheek; white throat. Lateral portion of body, gray/blue ground color with anterior portion of scales outlined in yellow; three black spots: supra-pectoral spot below 11-13th scale separate from upper lateral line and about same size of supra-anal spot; supra-anal spot at 21-23rd scale above and in contact with lower lateral line and covering 2-3 scales; caudal spot same diameter as supra-anal spot on caudal base; two vertical bars between supra-pectoral spot and dorsal-fin origin. Belly white. Dorsal fin clear with pale yellow spots and micro-melanophores; orange lappets. Caudal fin clear with scattered micro-melanophores and pale yellow spots. Anal fin clear with scattered micro-melanophores with median gray band; 6-8 pale yellow ocelli. Pectoral fin clear. Pelvic fin clear with scattered micro-melanophores.

Distribution and field observations. The distribution of *C. cyanocephalus* includes the rocky shores a few kilometers north of Meponda (Fig. 1; 13°22.391'S 34°50.186'E) to the Lumessi River (Fig. 1; 13°09.664'S 34°47.861'E).

Territorial males defend bowers at depths of 15-22 m. The spawning site is underneath a rocky ledge from which the sand has been excavated and deposited in front of the cavity's opening. There is hardly a bowl with a rim visible; the sand is just carried away from the spawning hole. The rock used in such constructions is almost always larger than the bower's diameter, which is 18-28 cm. The entrance to the spawning cavity is 4-5 cm high. Females live in small groups and are normally found within a meter from the bottom.

Etymology. From the Greek kyanos (greenish blue) and kephalo (head); refers to the green highlights throughout the head of breeding males; noun in apposition.

***Copadichromis parvus*, new species**
(Figs. 11, 12c)

Copadichromis sp. "verduyni dwarf", Konings, 2001: 315.

Holotype. PSU 3648, 87.2 mm SL; Mozambique: Lake Malaŵi: Lumessi, 13°08.196'S 34°47.844'E; J. R. Stauffer & A. F. Konings, 14 Feb 2002.

Paratypes. PSU 3649, 18; UMBC 009, 1, 64.1-96.0 mm SL; data as for holotype.

Diagnosis. *Copadichromis parvus* is distinguished from the other species of the *C. mbenjii* group by the possession of three lateral spots on the body (vs. two in *C. diplostigma* and one in *C. pleurostigma*) and a supra-pectoral spot that is about the same size as the supra-anal spot (vs. 2-2.5 times in *C. mbenjii* and *C. chizumuluensis* and about 1.5 times in the other species except *C. melas* and *C. cyanocephalus*). It is distinguished from *C. melas* by two vertical bars between the supra-pectoral spot and the opercle (vs. three). It is distinguished from *C. atripinnis* by the lack of a black submarginal band in the dorsal fin. Males in breeding coloration are distinguished from those of all other species in the *C. mbenjii* group by a black anal fin lacking a colored marginal band, except

from those of *C. melas*. It is distinguished from latter by the white to blue colored blaze on the head (vs. uniformly (black) colored head in *C. melas*).

Description. Morphometric and meristic data in Table 4. A small cichlid (Figs. 11, 12c) with dorsal snout profile straight; gape inclination of mouth about 40° to horizontal; jaws isognathous. Teeth on dentary and premaxilla in three rows; outer

Table 4. Morphometric and meristic values of *Copadichromis cyanocephalus* and *C. parvus*. Range includes holotype. H, holotype.

	<i>C. cyanocephalus</i> Charley's Bay, Mozambique (n=20)		<i>C. parvus</i> Lumessi, Mozambique (n=20)	
	H	range	H	range
Standard length, mm	90.2	66.3-90.2	87.2	64.1-96.0
Head length, mm	28.8	21.6-28.8	28.2	21.6-30.3
Percent standard length				
Head length	31.9	31.5-34.4	32.3	30.2-34.7
Body depth	34.5	34.3-37.2	35.1	33.5-38.2
Snout to dorsal-fin	34.9	34.9-39.3	35.2	33.8-40.7
Snout to pelvic-fin	38	37.1-42.8	40.9	38.0-43.9
Dorsal-fin base length	57.6	55.5-62.0	57.8	53.0-60.6
Anterior dorsal to anterior anal	50.7	49.4-56.8	51.2	47.5-54.1
Anterior dorsal to posterior anal	61.1	59.5-65.6	61.7	47.5-54.1
Posterior dorsal to anterior anal	30.9	29.4-34.0	32.4	29.0-35.0
Posterior dorsal to posterior anal	15.1	14.8-18.0	15.5	14.9-19.2
Posterior dorsal to ventral caudal	19.7	17.3-22.0	19.1	18.0-20.2
Posterior anal to dorsal caudal	20.1	19.9-23.2	20.4	19.3-23.0
Anterior dorsal to pelvic-fin origin	36.9	35.8-40.6	38.5	35.4-40.4
Posterior dorsal to pelvic-fin origin	54.4	54.1-58.2	57.6	51.2-59.8
Caudal peduncle length	17.1	14.3-19.2	15.8	13.2-18.0
Least caudal peduncle depth	11.9	11.1-13.5	12.3	10.5-13.3
Percent head length				
Snout length	29.2	26.6-31.7	30	27.4-32.1
Postorbital head length	38	33.7-38.9	37.8	33.1-39.0
Horizontal eye diameter	35.2	34.5-38.6	33	32.6-40.4
Vertical eye diameter	34	33.4-38.9	33	32.0-38.5
Head depth	98.1	86.4-101.3	99.9	81.4-100.3
Preorbital depth	18.2	13.9-18.2	16.2	13.6-18.5
Cheek depth	20.5	15.2-21.2	22.4	15.6-25.4
Lower jaw length	41.5	33.4-41.5	39.3	36.3-42.5
Counts				
Dorsal-fin spines	16	16-17	17	15-17
Dorsal-fin rays	11	10-11	10	10-12
Anal-fin spines	3	3	3	3
Anal-fin rays	9	8-9	8	8-9
Pelvic-fin rays	5	5	5	5
Pectoral-fin rays	13	13-14	13	12-14
Lateral line scales	33	32-34	32	32-33
Pored scales posterior to lateral line	2	1-2	2	0-3
Scale rows on cheek	3	2-3	3	2-3
Gill rakers 1 st ceratobranchial	14	12-16	13	12-17
Gill rakers 1 st epibranchial	6	5-6	5	5-6
Teeth outer left lower jaw	12	10-14	12	11-15
Teeth rows upper jaw	3	3	3	3
Teeth rows lower jaw	3	3	3	3



Fig. 12. **a**, *Copadichromis insularis*, breeding male, not preserved, approx. size 85 mm SL; Malawi: Nakantenga Island; **b**, *C. cyanocephalus*, territorial male, not preserved, approx. size 85 mm SL; Mozambique: Chiloelo; **c**, *C. parvus*, breeding male, not preserved, approx. size 85 mm SL; Mozambique: Metangula.

row with small bicuspid teeth in juveniles and females; large unicuspid teeth in mature males. Pharyngeal jaws not examined. Gill rakers short.

Coloration. Breeding males: head dark blue with light blue blaze with green highlights to origin of dorsal fin; cheek dark green; preorbital and throat black. Black opercle spot. Lateral portion of body, dark blue ground coloration dorsally; blue/green ventrally; breast blue/black; 7-8 black bars; gray belly. Proximal one-third of dorsal fin black, mid one-third blue, and distal one-third light blue with orange lappets. Caudal fin with black rays and blue membranes. Anal fin black. Pectoral fin with black rays and clear membranes. Pelvic fin black with white leading edge.

Females: head gray with white cheek with blue/purple highlights; throat white. Lateral portion of body gray dorsally; white ventrally; three black spots: supra-pectoral spot below 10-12th scale not in contact with upper lateral line and about same size of supra-anal spot; supra-anal spot at 24-26th scale above and in contact with lower lateral line and covering 2-3 scales; caudal spot same diameter as supra-anal spot on caudal base; two vertical bars between supra-pectoral spot and dorsal-fin origin; anterior portion of scales yellow, posterior portion blue/gray; white belly. Dorsal fin pale blue/gray with gray spots and yellow/orange lappets. Proximal one-third of caudal fin dark gray, distal two-thirds light gray. Anal fin clear with scattered micro-melanophores. Pectoral fin clear. Pelvic fin with first three membranes gray, white leading edge, and remainder clear.

Distribution and field observations. *Copadichromis parvus* is the most widely distributed species of this group. Its distribution's southernmost point is just north of the Chiloele River (Fig. 1; 13°12.592'S 34°48.657'E), where it shares the sand/rock interface with *C. cyanocephalus*, to the bay north of Metangula (Fig. 1; 12°41.294'S 34°48.294'E), all in Mozambique.

Territorial males occur at depths of 11-23 m and construct bowers by excavating sand from beneath rocks. Their bowers have a diameter of 15-22 cm and the entrance to the cavity has a height of 3.5-6 cm. Most often the rock in the construction is larger than the bower's diameter and spawning takes place inside the cavity. On sandy bottoms there is a shallow bowl-shaped 'frontage' to the cavity but in softer bottoms no

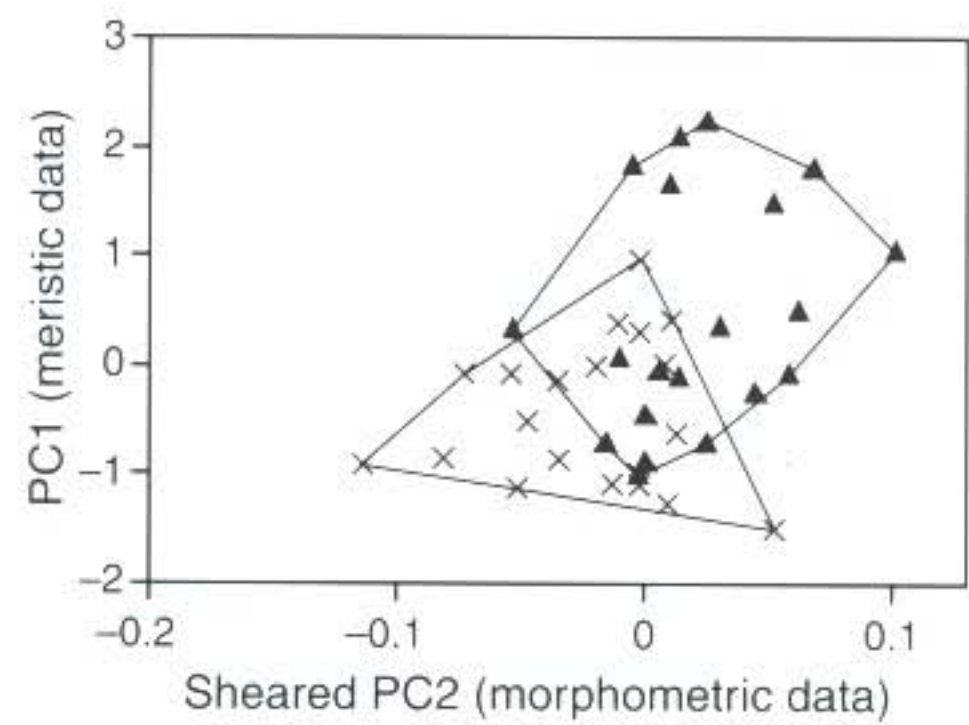


Fig. 13. Plot of first principal component of meristic data and second sheared principal component of the morphometric data of *Copadichromis parvus* (x) and *C. cyanocephalus* (▲).

bowl-shaped entrance to the spawning cavity is present. Foraging females and non-territorial males feed in the open water column 1-3 m off the bottom and on benthic invertebrates. Mouth-brooding females are solitary and remain close to the substrate.

Remarks. *Copadichromis cyanocephalus* and *C. parvus* occur sympatrically between Chiloele and Lumessi along the Mozambique shore of the lake (Fig. 1). Although we could distinguish the two species by the male breeding coloration (blue in *C. cyanocephalus* and blue-black with a white to light-blue blaze on the head in *C. parvus*), we could not find a single morphometric or meristic character in individuals of these two populations, which did not overlap. The minimum clusters formed by plotting the PC1 of the meristic data against the SPC2 of the morphometric data, however, were significantly different along both axes ($p < 0.05$, ANOVA) although the polygons overlap (Fig. 13). Variables that had the highest loading on second principal components of the morphometric data were the distance between the dorsal-fin origin and the posterior edge of the anal fin (0.651), cheek depth (-0.407), and caudal-peduncle length (0.398); while those with the highest loadings on the principal components of the meristic data were dorsal-fin rays (0.592), gill rakers on the first ceratobranchial (0.521), and dorsal-fin spines (-0.471).

Etymology. From the Latin adjective *parvus* (small) to indicate the small size of this species when compared to other species of *Copadichromis*.

Key to species of *Copadichromis*

1. - Spots or blotches on body.
.....2
- No conspicuous markings.
.....24
2. - No supra-pectoral spot.
.....*C. cyaneus*
- Conspicuous supra-pectoral spot.
.....3
3. - Supra-anal spot faint or absent.
.....4
- Supra-anal spot conspicuous unless masked
by male breeding coloration.
.....9
4. - Females and immature males with hyaline
anal fin.
.....5
- Females and immature males with bright
yellow anal fin.
.....8
5. - Supra-pectoral spot small, not wider than
three times the width of a vertical bar (2-3
scales).
.....*C. jacksoni*
- Supra-pectoral spot large, wider than four
times the width of a vertical bar (4-5 sca-
les).
.....6
6. - 13-19 gill rakers on first ceratobranchial.
.....*C. diplostigma*
- 23-28 gill rakers on first ceratobranchial.
.....7
7. - Length of caudal peduncle 13.1-14.6 % SL.
.....*C. geertsi*
- Length of caudal peduncle 14.7-18.0 % SL.
.....*C. likomae*
8. - 17-18 gill rakers on first ceratobranchial.
.....*C. pleurostigma*
- 22-25 gill rakers on first ceratobranchial.
.....*C. pleurostigmoides*
9. - Females and immature males with bright
yellow or orange anal fin.
.....10
- Females and immature males with hyaline
anal fin.
.....11
10. - 19-22 gill rakers on first ceratobranchial.
.....*C. borleyi* (part)
- 15-18 gill rakers on first ceratobranchial.
.....*C. trimaculatus*
11. - 24-27 on first ceratobranchial.
.....*C. quadrimaculatus*
- 10-23 gill rakers on first ceratobranchial.
.....12
12. - Supra-pectoral spot 2-2.5 times supra-anal
spot.
.....13
- Supra-pectoral spot 1-1.5 times supra-anal
spot.
.....15
13. - 12-15 gill rakers on first ceratobranchial.
.....*C. mbenjii*
- 16-23 gill rakers on first ceratobranchial.
.....14
14. - 25-27 total rays in dorsal fin, supra-anal spot
smaller than caudal spot.
.....*C. chrysonotus*
- 27-29 total rays in dorsal fin, supra-anal spot
larger than caudal spot.
.....*C. chizumuluensis*
15. - Supra-pectoral spot 2-3 scales in diameter,
separate from upper lateral line.
.....16
- Supra-pectoral spot 4-6 scales in diameter,
in contact with or across upper lateral
line.
.....20
16. - Supra-pectoral spot about same size as
supra-anal spot.
.....17
- Supra-pectoral spot 1.2-1.5 times diameter
supra-anal spot.
.....*C. azureus* (part)
17. - Black submarginal band in dorsal fin.
.....*C. atripinnis*
- Black submarginal band in dorsal fin la-
cking.
.....18

18. - Three vertical bars between operculum and supra-pectoral spot.
.....*C. melas*
- Two vertical bars between operculum and supra-pectoral spot.
.....19
19. - Breeding males with white-blue blaze on head.
.....*C. parvus*
- Breeding males lacking white blaze on head.
.....*C. cyanocephalus*
20. - Supra-anal spot in contact with or across upper lateral line.
.....*C. insularis*
- Supra-anal spot separate from upper lateral line.
.....21
21. - Supra-anal spot 1-1.5 scales wide.
.....*C. azureus* (part)
- Supra-anal spot 2-4 scales wide.
.....22
22. - Depth of body 30.3-34.4 % SL.
.....*C. nkatae*
- Depth of body 34.4-38.4 % SL.
.....23
23. - Breeding males with yellow breast and blue anal fin.
.....*C. verduyni*
- Breeding males with black or blue-black breast and black anal fin.
.....*C. trewavasae*
24. - Depth of body 28.1-32.3 % SL.
.....*C. mloto*
- Depth of body 34.4- 42.3 % SL.
.....25
25. - Females and immature males with yellow to red anal fins; adult males with long pelvic fin, length 52-65 % SL.
.....*C. borleyi* (part)
- Anal fins hyaline in females and immature males; length of pelvic fin in breeding males 32-38 % SL.
.....26

26. - Body depth 38-42 % SL; snout 26-29 % length of head.
.....*C. virginalis*
- Body depth 34-38 % SL; snout 29-33 % length of head.
.....*C. ileisi*

Mchenga, new genus

Copadichromis eucinostomus species group, Stauffer et al., 1993: 1017.

Type species. *Copadichromis cyclicos* Stauffer, LoVullo & McKaye 1993: 1020.

Diagnosis. *Mchenga* is comprised of a series of small and slender cichlid fishes endemic to Lake Malaŵi frequenting shallow water (between 3-25 m deep) habitats characterized by sandy bottoms. The low number of gill rakers (10-18) on the first ceratobranchial, a protrusible mouth that can form a sucking tube, and the lack of spots or stripes on the body distinguish species of *Mchenga* from all other Malaŵi genera, except *Copadichromis*. Males of *Mchenga* have small bicuspid teeth in the outer row of the upper and lower oral jaws while males of *Copadichromis* have enlarged unicuspid teeth in the outer row of both these jaws. Male *Mchenga*, for those species we have field observations, build bowers on the lake bottom in sandy habitats. In extensive leks with many males holding a bower, some males may build a bower on top of large boulders if these are in the vicinity. Such boulders are merely used as bottom substrate and the rock does not interrupt the rim of these bowers (Fig. 14) distinguishing them from those species of *Copadichromis* that build bowers, i.e. all members of the *C. mbenjii* group. We regard the independence of the rocky habitat for breeding purposes as the most derived character of the species of *Mchenga*. They were initially included in *Copadichromis* (see Discussion).

Two species, *M. eucinostomus* and *M. inornata*, are only known from the type specimens and their breeding biology is unknown. They were placed in *Mchenga* based on the presence of small bicuspid teeth on the outer jaws of adult males.

Etymology. *Mchenga*, from Chichewa, the indigenous language of Malaŵi; mchenga (sand), was chosen to indicate the type of bowers constructed by the members of this genus. Gender is feminine.



Fig. 14. *Mchenga cyclicos*, male on bower; Malaŵi: Msuli Point.

Mchenga cyclicos (Stauffer, LoVullo & McKaye)

Diagnosis. The low number of gill rakers (10-12) distinguishes this species from the other members of the genus except *M. thinos*. It differs from *M. thinos* by the lack of yellow ocelli on the anal fin of females and non-breeding males. Breeding male *M. thinos* lack the black markings in the caudal fin that are present in those of *M. cyclicos*. The teeth in the outer rows on dentary and premaxilla of mature males are small and bicuspid. Other descriptive, distribution, and ecological data published in Stauffer et al. (1993).

Mchenga eucinostomus (Regan)

Diagnosis. Differs from other *Mchenga*, except *M. flavimanus*, by having 17 (n=2) gill rakers on the first ceratobranchial. It differs from the latter species by a larger premaxillary pedicel (37-40 % vs. 30-36 % HL in *C. flavimanus*). The teeth in the outer rows on dentary and premaxilla of both types are small and bicuspid. Other descriptive data published in Regan (1922) and Stauffer et al. (1993).

Mchenga inornata (Regan)

Diagnosis. The possession of 15-16 gill rakers on the first ceratobranchial distinguishes this species from other members of the genus except *M. conophoros*. It differs from the latter species by a shallower preorbital (16.7-17.5 vs. 18.1-22.1 % HL in *M. conophoros*). The teeth in the outer rows on dentary and premaxilla of mature males are small and bicuspid. Other descriptive data published in Regan (1922).

Mchenga flavimanus (Iles)

Diagnosis. Distinguished from all other species of *Mchenga* by the presence of yellow fins in juveniles and mature females. It is distinguished from *M. eucinostomus* by the possession of a smaller premaxillary pedicel (30-36 vs. 37-40 % HL). The teeth in the outer rows on dentary and premaxilla of mature males, females, and immatures are small and bicuspid. Other descriptive data published in Iles (1960).

***Mchenga conophoros* (Stauffer, LoVullo & McKaye)**

Diagnosis. The possession of 13-16 gill rakers distinguishes this species from other members of the genus except *M. thinos* and *M. inornata*. It differs from *M. thinos* by the lack of yellow ocelli on the anal fin of females and non-breeding males. Breeding males of *M. thinos* lack the black markings in the caudal fin that are present in breeding males of *M. conophoros*. It differs from *M. inornata* by a deeper preorbital (18.1-22.1 vs. 16.7-17.5 % HL). The teeth in the outer rows on dentary and premaxilla of mature males are small and bicuspid. Other descriptive, distribution, and ecological data published in Stauffer et al. (1993).

***Mchenga thinos* (Stauffer, LoVullo & McKaye)**

Diagnosis. It is distinguished from *M. conophoros*, *M. inornata* and *M. cyclicos* by the yellow ocelli on the anal fin of females and non-breeding males. Breeding male *M. thinos* lack the black markings in the caudal fin that are present in breeding males of *M. cyclicos* and *M. conophoros*. It has 10-16 gill rakers, which distinguishes it from *M. eucinostomus* (17 gill rakers in two types). Juveniles and females have hyaline fins which distinguish them from those of *M. flavimanus*, which have yellow fins. The teeth in the outer rows on dentary and premaxilla of mature males are small and bicuspid. Other descriptive, distribution, and ecological data have been published in Stauffer et al. (1993).

Key to species of *Mchenga*

- 1. - 17-18 gill rakers on first ceratobranchial.2
- 10-16 gill rakers on first ceratobranchial.3
- 2. - Premaxillary pedicel 37-40 % HL.*M. eucinostomus*
- Premaxillary pedicel 30-36 % HL.*M. flavimanus* (in part)
- 3. - Fins of juveniles and mature females yellow.*M. flavimanus* (in part)
- Fins of juveniles hyaline.4

- 4. - Yellow ocelli in anal fin of females.*M. thinos*
- Females with clear anal fin or with micro-melanophores.5
- 5. - 13 or more gill rakers on first ceratobranchial.6
- 10-12 gill rakers on first ceratobranchial.*M. cyclicos*
- 6. - 13-15 gill rakers on first ceratobranchial; preorbital depth 18.1-22.1 % of head length.*M. conophoros*
- 15-16 gill rakers on first ceratobranchial; preorbital depth 16.7-17.5 % of head length.*M. inornata*

Discussion

The current classification of Malaŵi cichlids is largely based on basic pigmentation patterns and we concur with previous workers on these fishes (Trewavas 1935; Eccles & Trewavas 1989) that these patterns are useful characters to indicate relationships among the various genera. In this light, we regard *Copadichromis* as a polyphyletic genus because it includes groups with spotted and those with non-descript species. We have removed one group of non-descript species, *Mchenga*, from *Copadichromis* as we found them significantly different in basic melanin pattern, number of gill rakers, and shape of body, from the type species of this genus (i.e. *C. quadrimaculatus*). In addition to these morphological characters, we found that habitat preference and bower construction differ significantly from those of the current members of *Copadichromis*.

Stauffer et al. (1993) demonstrated that the shape and composition of the bower is a manifestation of a behavioral trait and used bower shape to delimit taxonomic groupings within the Lake Malaŵi species flock. The construction of the bower by the male is complex and appears to be driven by female choice (Kellogg et al., 2000); thus, we believe that, in line with the evolutionary species concept, similarities of bower shape and construction strategies among species can be used as indicators to infer relationship within the Malaŵi plankton-feeders. We were unable, however, to formulate an adequate diagnosis primarily

based on the behavioral trait of bower construction for the species we have placed in the *C. mbenjii* and in the *C. virginalis* group.

Copadichromis geertsi, currently placed in the *C. quadrimaculatus* group based on morphological grounds (deep body and high gill raker count), does not fit in the *C. mbenjii* group, but *C. geertsi* does construct bowers. The association with the rocky habitat, at least during the breeding phase, unites the members of the *C. quadrimaculatus*, *C. mbenjii*, and *C. virginalis* groups, but because behavioral observations are not available for all species involved, a more accurate diagnosis of *Copadichromis* is not possible at this time.

The male haplochromine cichlid in Lake Malawi is confronted with two conflicting objectives regarding his breeding strategy: advertise to females announcing his vigor and readiness to spawn, and secure a protected (from egg robbers) site where deposition of eggs shall take place. Our observations indicate that egg predators are far more abundant in the rocky habitat than in the sandy habitat. In principle, every cichlid in the lake, large or small, is a potential egg predator and rocky environments afford even small species a chance to come within striking distance of eggs laid by open rock spawning *Copadichromis*. Species of *Copadichromis* breeding in rocky areas use quarters that are less desirable to the potential egg robbers of this habitat (Robinson & Ribbink, 1998), i.e. the exposed surfaces of large boulders that offer little to no protection to the small haplochromines (mbuna) that are this habitat's principal residents. Species of *Copadichromis* often spawn along the vertical face of a boulder or under an overhanging ledge where the shade affords additional protection from egg robbers. Nevertheless, spawning on boulders in the rocky habitat brings on a heavy burden to territorial males that have to maintain their spawning areas free of potential egg predators.

We regard the dependence on large boulders in pure rocky habitats as a breeding locale, as the most ancestral behavioral trait within *Copadichromis*, because we perceive this as the most energy-consuming strategy. Among the species of the *C. quadrimaculatus* group we recognize two derived traits to cope with the hostile environment of the pure rocky habitat: one is free-water spawning and the other is breeding during a particular time of the year, i.e. short breeding season during which almost all adult members of the population breed. The latter trait, recorded from *C. quadrima-*

culatus only (Fryer & Iles, 1972), but other species may employ this strategy as well, e.g., this strategy is also known for *C. ileisi* and *C. virginalis* of the *C. virginalis* group. The temporary presence of huge numbers of breeding utaka in the rocky habitat arguably alleviates the predation pressure on single spawns. Only one species, *C. chrysonotus*, is known to spawn in the water column, away from rocks and this derived spawning behavior may make it more difficult for predators to target eggs.

The abandoning of the rocky habitat to a less hostile environment appears beneficial for species of the *C. mbenjii* group. The principal diagnostic characteristics of this group are the construction of a sand bower that includes a rock (Figs. 3b, 5b, 6b, 8b, 9b, 11b) and spawning at the sand/rock interface. One of the advantages of a bower is that it affords a sheltered spawning site, which may not be available in the rocky habitat. Moreover, the construction of a sand bower enables males of this group also to advertise to females by the size and shape of the structure in addition to courtship behavior. Thus, the construction of a bower, i.e. a protected spawning site away from the pure rocky habitat, by members of the *C. mbenjii* group is considered to be a derived character.

A species we have not included in the *C. mbenjii* group is *C. borleyi*. Males of *C. borleyi*, in most populations, defend spawning sites on large boulders. Some males, in some southern populations that occur in shallow habitats without large boulders, spread fine sand over their territories, possibly enhancing visibility of their spawning sites (Konings, 2001). Males of *C. borleyi* move sand differently than males of the *C. mbenjii* group; instead of starting in the center of the spawning platform, they evenly spread fine sand over the entire spawning site. They do so by passing fine material through their gills and let it settle on the rock. In our opinion, this is intrinsically different from that of the members of the *C. mbenjii* group. Males of these species start to dig their spawning bowl in the center of the dish and transport surplus sand to its edge. Even when males use additional sand from the environment, it is first brought to the center of the pit and then deposited on the edge. The individuals of some southern populations of *C. borleyi* lack spots on the flank.

The relationship of *C. likomae* with other members of *Copadichromis* is not yet clarified. Unlike the other members of *Copadichromis*, how-

ever, male *C. likomae* build sand bowers without rocks, similar to those of *Mchenga*. The presence of large unicuspid teeth in mature males, 24-28 gill rakers on the first ceratobranchial, and a supra-pectoral and a caudal spot align it morphologically with the *C. quadrimaculatus* group. We therefore leave this species in *Copadichromis*.

The diagnostic behavioral character of the species in *Mchenga* is the sand bower in shallow water that does not include a rock (Fig. 14). In addition to male coloration, olfactory cues, and courtship behavior, mate recognition can also be achieved by the assessment of the structure and position of the male's bower. Sexual selection is thought to play a major role in speciation of the Malaŵi cichlid fauna (Genner & Turner, 2005) and since members of *Mchenga*, when compared to those of *Copadichromis*, have an additional trait operating in the mate recognition process we believe that they are on a different path in the phylogeny. We consider that species of *Mchenga* represent a monophyletic group of Lake Malaŵi cichlids and that the shape, position of the bower on the sand, and construction of the bower in the absence of a rock interrupting the rim are synapomorphies (Stauffer et al., 1993). Stauffer et al. (1995) also noted that the bowers of *Mchenga* are structurally different from those of *Tramitichromis*, *Lethrinops*, and *Taeniolethrinops*. The construction of the bower by male *Mchenga* is commenced by the addition of sand from the surrounding substrate rather than an excavation of the sand, as performed by members of the *C. mbenjii* group.

Mchenga inornata and *M. flavimanus*, are also placed in *Mchenga*, because they share two of the diagnostic traits, i.e. small bicuspid teeth in the outer row of the oral jaws of mature males and the lack of lateral spots. These species, however, have not yet been observed spawning in their natural setting (they have not yet been recognized in the field), which is necessary to assess the character of their spawning sites. The lack of lateral spots and the possession of a protrusible mouth could, as well, place them in the less well defined *C. virginalis* group, but the low number of gill rakers on the first ceratobranchial and the presence of small bicuspid teeth in the outer tooth rows of adult males support their placement in *Mchenga*.

The sister group of *Mchenga* could possibly be *Nyassachromis* because they share several behavioral characters, i.e. bower construction on the

sand using similar building techniques, preference for shallow sandy habitats, and foraging in large schools near the bottom. Also morphologically they are similar: slender body, small bicuspid teeth in outer row of oral jaws, and a moderate number of gill rakers (10-19 for species in both genera). The basic pigmentation pattern, a key element in the classification of Malaŵi cichlids, however differs. *Nyassachromis* usually exhibits a prominently pigmented mid-lateral band, with sometimes additional horizontal elements in the dorso-lateral band, while members of *Mchenga* lack any spots or bands on the body.

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